MICROCOPY RESOLUTION TEST CHART
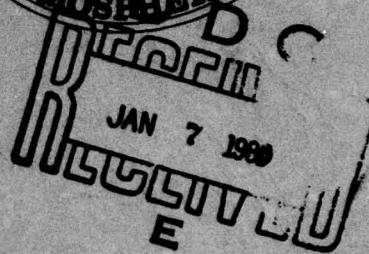
AD A078642

TECHNICAL REPORT

LEVEL

UNDERWATER SOUND: A REVIEW OF ITS EFFECTS ON SHARKS

By Arthur A. Myrberg, Jr.

UM-RSMAS-79004

80- 7 1 008

UNIVERSITY OF MIAMI
ROSENSTIEL SCHOOL OF MARINE AND ATMOSPHERIC SCIENCE
4600 Rickenbacker Causeway
Miami, Florida 33149

TECHNICAL REPORT, Apr 78 - Dec 79,

December 1979   55

UNDERWATER SOUND: A REVIEW OF ITS

EFFECTS ON SHARKS.

by

Arthur A. Myrberg, Jr.

UM-RSMAS-79004

William W. Hay
Dean

Reprinted From

Sensory Biology of Sharks, Skates, and Rays

1978

UNDERWATER SOUND—ITS EFFECT ON THE
BEHAVIOR OF SHARKS

ARTHUR A. MYRBERG, JR.

Rosenstiel School of Marine and Atmospheric Science
University of Miami, Miami Florida 33149

INTRODUCTION

Divers who frequent areas where sharks prevail have long known that spearfishing greatly increases the chance of a shark encounter. Stories of such encounters often are surprisingly similar, regardless of geographical location. Usually sharks are not seen when the fish is speared but appear suddenly a few moments later. In the few cases in which their approach is noted, the rapidly moving predators often come from directions where chemical information could not possibly have reached them, due to the prevailing current or the extremely brief time between the spearing and their arrival. The approaching sharks appear well oriented; they locate the struggling fish within seconds, whether in the open or hidden in a recess of the reef. Such orientation appears clearly to depend, however, on the struggling movements of the speared fish. If the fish rests quietly, sharks only a few meters upstream show no interest.

These accounts, as well as those from the literature (e.g., Eibl-Eibesfeldt and Hass 1959, Hass 1959, Hobson 1963, Limbaugh 1963, Wright 1948), clearly suggest that sharks can, indeed, be attracted solely by the sounds of struggling fishes. This suggestion was first tested by Nelson and Gruber (1963, see also Wisby et al. 1964), who showed that the sounds of struggling produced by a speared grouper consist of rapid pulses of broadband noise with peak energy below 100 Hz and that similar sounds can attract several species of free-ranging sharks. Playback of rapid pulses of noise with frequencies below 60 Hz were especially effective in that regard, while sounds at these same frequencies but without pulsing or with pulsed noise bands between 400 and 600 had no effect.

These findings were discussed during the Second Symposium on Marine Bioacoustics at New York City in April 1966, when several speakers commented that attempts to confirm such attraction by a variety of underwater sounds had failed. These remarks immediately followed another discussion that ended with most of those present accepting the idea that fishes are incapable of orienting to a sound source located beyond the region of the near-field effect.[1] Since the published report on shark attraction included the important point that the rapidly approaching animals appeared well oriented to the sound source, such responses, if real, could have occurred only within the near-field of the sound. Yet the distances mentioned in the original reports (e.g., Wisby and Nelson 1964) strongly suggested that oriented movements had begun beyond that region. This difficulty, as well as the lack of confirmation, resulted in the opinion that confirmation of such results was

---

[1]This effect consists of the relatively large amplitude excursion of the medium close to a sound source that is associated either with movement of the source in excess of the compressibility of the medium or with the curvature of the wave front. Attenuation of this effect occurs faster than does attenuation of particle motion associated with pressure fluctuations; thus the near-field effect predominates only within a region generally extending less than one wavelength from the source; beyond that point, one enters the far-field (see Banner 1972, van Bergeijk 1964).

needed before serious consideration could be given to the perplexing problem of far-field orientation by sharks.

Clear confirmation of those results appeared shortly thereafter when, fortunately, field experiments were again conducted on several species of sharks frequenting the underwater television site of the Bimini (Bahamas) Video-Acoustic Installation (Myrberg et al. 1969, Richard 1968) and other locations in Bahamian and Florida waters (Banner 1968, Nelson et al. 1969). These independent studies established that certain kinds of underwater sound are highly attractive to various species of sharks and that such attraction can be initiated in the far-field.

Generally, long periods of time must pass before results from field tests can be reexamined by appropriate tests of confirmation. Fortunately this has not been the case with this question even though tests have often involved large, highly mobile animals. Various findings regarding the acoustic biology of free-ranging sharks have been repeatedly confirmed by the independent studies of Nelson and his coworkers, who used Pacific species (Nelson and Johnson 1970, 1972; Nelson et al. 1969), and by those of our team, using primarily Atlantic species (Banner 1968, 1972; Myrberg 1969, 1972; Myrberg et al. 1969, 1972, 1975a, 1976). Such confirmation has assuredly posed additional questions and hypotheses from knowledge only recently gained, but it has been necessary, since the research has had implications regarding human safety.

SHARKS AND SOUNDS—A STORY WITH MANY IMPLICATIONS

The story that has unfolded during the last few years regarding the effects of sound on the behavior of sharks encompasses a wide variety of diverse yet interrelated topics. They include biophysical and ecological considerations, learning and orientation processes, and even neural events at the level of the sensory receptors. To highlight the most interesting points, this part of the report is divided into a number of sections, each centering on one topic. The entire story, as we at present understand it, includes information extending beyond what can be covered under a few arbitrarily chosen headings. Therefore, where necessary, an attempt has been made to explain interrelationships that bridge the topics covered. The first section deals with the types of sharks that have been attracted to sound sources; the second and third center on the physical factors that appear to be important or unimportant for an acoustic attractant; the fourth highlights the behavior of sharks in the vicinity of a sound source; the fifth deals with those qualities of sound that apparently promote a response opposite to attraction, i.e., withdrawal; and the last section centers on the perplexing problem of directional hearing in sharks.

The Species List for Attraction

All species of sharks that have been examined in the field (Table 1) have been found to be attracted to specific types of synthesized sounds as well as

Table 1.   Summary of experiments in which sharks were attracted to an underwater transducer (speaker) during playback of low-frequency, pulsed sounds.*

Family and species	Common name	Sound†	Author(s)
Alopidae			
Alopias sp.	Thresher	HF (N)	Nelson & Johnson (unpublished)
Carcharhinidae			
Carcharhinus sp.		FN (A)	Nelson & Gruber 1963
		FN (A)	Richard 1968
		FN, SqW (A)	Myrberg et al. 1969
C. albimarginatus	Silvertip	FN (A)	Nelson & Johnson 1972
C. falciformis	Silky	FN (A)	Nelson et al 1969
		SpF (N)	Evans & Gilbert 1971
		FN (A)	Myrberg et al. 1972
			Myrberg et al. 1975a
			Myrberg et al. 1975b
			Myrberg et al. 1976
C. leucas	Bull	FN (A)	Nelson & Gruber 1963
C. longimanus	Oceanic whitetip	FN (A)	Myrberg et al. 1975a
			Myrberg et al. 1975b
			Myrberg et al. 1976
C. melanopterus	Blacktip reef	FN (A)	Nelson & Johnson 1970
		FN (A)	Nelson & Johnson 1972
C. menisorrah	Gray reef	SpF (N)	Brown 1968
		FN (A)	Nelson & Johnson 1970
		FN (A)	Nelson & Johnson 1972
C. springeri	Reef	FN, SqW (A)	Myrberg et al. 1969
Galeocerdo cuvieri	Tiger	FN (A)	Nelson & Gruber 1963
Negaprion brevirostris	Lemon	FN (A)	Nelson & Gruber 1963
		BbN (A)	Banner 1968
		FS (N)	Banner 1972
Negaprion fosteri	"Lemon"	FN (A)	Nelson & Johnson 1972
Prionace glauca	Blue	HF, StF (N)	Nelson & Johnson
		FN (A)	(unpublished)
Rhizoprionodon porosus	Sharpnose	FN (A)	Richard 1968
		FN, SqW (A)	Myrberg et al. 1969
Triaenodon obesus	Reef whitetip	SpF (N)	Brown 1968
		SpF, StF (N)	
		FN (A)	Nelson & Johnson 1970
		FN (A)	Nelson & Johnson 1972
Lamnidae			
Isurus oxyrinchus	Mako	HF, StF (N)	Nelson & Johnson (unpublished)
Orectolobidae			
Ginglymostoma cirratum	Nurse	FN (A)	Richard 1968
		FN, SqW (A)	Myrberg et al. 1969
		FN (A)	Nelson et al. 1969
Sphyrnidae			
Sphyrna sp.	Hammerhead	FN (A)	Nelson & Gruber 1963
S. tiburo	Bonnethead	FN (A)	Nelson et al. 1969

*Taken in part from Nelson and Johnson 1972.
†Types of artificially produced (A), and naturally recorded (N) pulsed sounds: FN, filtered random or white noise; BbN, broadband noise; SqW, square waves; SpF, speared struggling fish; HF, hooked struggling fish; StF, stampeded group of fish; and FS, fish sounds.

to a variety of biological sounds. The group includes species commonly found over shallow flats and reefs as well as over deep oceanic waters. Most are piscivorous, but the group also includes a number of small species that feed mainly on certain invertebrates (e.g., the bonnethead, *Sphyrna tiburo*). The attractiveness of such sounds to sharks of such diverse habits suggests strongly that most, if not all, other carnivorous sharks will react similarly to appropriate underwater sound sources. It is noteworthy that other carnivorous fishes, such as groupers and snappers, find the same types of underwater sounds attractive, although their approach to the sources is much slower than that of sharks (Myrberg et al. 1969, Nelson and Johnson 1970, Nelson et al. 1969, Richard 1968, Steinberg et al. 1965).

Qualities of Attractive Sound

Early experiments showed that not all sounds elicit approach in sharks. This suggested that such animals are attending to specific qualities of transmissions. To determine these qualities, we synthesized sounds to control systematically those features of obvious interest. By this means alone or with natural and synthesized sound used together in the same experimental design, findings from the field related closely to the meager but significant results previously obtained on the hearing physiology of some sharks.

Spectral Content—One important feature of an attractive sound was its spectral content. All results indicated that a sound, to be attractive to sharks, must contain frequencies below 800 or 1000 Hz; if not, approach was not seen (e.g., Myrberg et al. 1969); see Figure 1. The initial findings by Nelson and Gruber (1963) suggested that only very low frequencies were attractive, i.e. below 60 Hz. This figure was revised upwards, however, after subsequent studies showed that signals possessing higher frequencies were also attractive (Myberg et al. 1972, Nelson and Johnson 1972). Yet, for those species most intensively studied (e.g., the silky shark, *Carcharhinus falciformis*), levels of attraction increased as the included wavelengths of a signal increased (Myrberg et al. 1972); see Table 2. This cline of responsiveness eventually ended in similar effectiveness when octave bands of very low frequencies were finally reached, i.e., 10 to 20 Hz and 20 to 40 Hz (Myrberg et al. 1975a, 1976). All synthesized sounds used during controlled testing, however, were bands of limited frequencies, and experiments have not yet determined the band limits of an attractive sound. Nevertheless, any signal whose spectrum includes an octave or more and contains frequencies below 800 Hz will be attractive—so long as it possesses a few additional qualities.

The upper frequency limit of attractive sound, around 800 to 1000 Hz, agrees well with data on the hearing abilities of those few species of sharks tested under reasonably controlled conditions (the lemon shark, *Negaprion brevirostris*—Banner 1967, Nelson 1967, Wisby et al. 1964; the bull shark, *C. leucas*—Kritzler and Wood 1961; the scalloped hammerhead, *S. lewini*—Olla 1962). It is noteworthy that this limit is extremely close to the upper limiting frequencies that elicit vestibular microphonics in another elasmo-
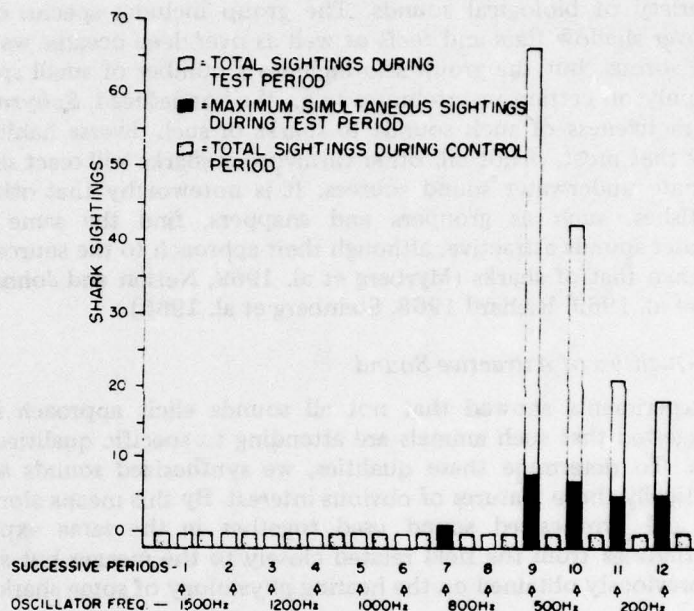
Figure 1 Attraction of sharpnose sharks *Rhizoprionodon*, sp., by acoustic signals, showing upper effective frequency limit. Signals consisted of irregularly pulsed, overdriven sine waves, having fundamental frequencies from 200 to 1500 Hz. Peak sound pressure level at 18.5 m from sound source was approximately 20 dB above broadband ambient noise. Each test and control period—3 min. (Myrberg et al. 1969)

branch, the skate, *Raja clavata*. Also, the most effective frequency range for purposes of attraction, between 10 and 100 Hz, approximates the range of frequencies associated with spike discharges from vibration-sensitive areas of the labyrinth in this skate (Lowenstein and Roberts 1951). Although the authors attached no physiological significance to their data, that their findings correlate with those of others at a different level of integration indicates a functional significance between these neural and behavioral events. Additional examination of hearing ability and its neural correlates in other elasmobranch fishes will certainly provide further insight into such a suggestion.

Pure tones, regardless of frequency, do not attract free-ranging sharks (Myrberg et al. 1969, Richard 1968). The scarcity of biologically produced pure tones in the aquatic environment may explain this failure to react, thus reinforcing the belief that the attraction response to low-frequency, broadband sounds has a biologically adaptive basis.

Repetitive Pulsing—The second quality of an attractive sound is its repetitive pulsing. Continuous sound, regardless of frequency, does not elicit

Table 2. Differential attraction of silky sharks by irregularly pulsed, instrumental signals of different frequencies (Straits of Florida).*

Session	Frequency band of signal (Hz)	No. of sessions	Surface area covered by signal (S/N=0)	Surface area covered by signal (S/N=20)	Total no. of sharks attracted	Actual no. of sharks per session	Relative level of attractiveness (predicted no.† ÷ actual no.)
Test							
	25-50	85	0.036 km²	0.0018 km²	29	0.34	918.9
	75-150	85	1.044 km²	0.046 km²	13	0.15	16.1
	250-500	85	43.32 km²	0.81 km²	20	0.24	1.5
	500-1000	85	36.75 km²	0.69 km²	12	0.14	0
Control							
	No signal	177	—	—	12	0.007	

*Modified from Myberg et al. 1972.

†If all signals were as attractive as the 500-1000 Hz signal (areas arbitrarily chosen are those having S/N = 20).

attraction (Hobson 1963, Nelson and Gruber 1963, Wisby et al. 1964, personal observation). Banner (1972) demonstrated in young lemon sharks that the rapidity of pulsing is directly related to the relative attractiveness of various biological sounds produced by their prey. This same correlation existed in silky sharks for synthesized sounds so long as their spectral content was appropriate (Myrberg et al. 1972). Although extremely low frequency signals cannot be pulsed rapidly and still maintain their spectral integrity, even a constant pulse rate of 1/s appears to be slightly attractive (Myrberg et al. 1972) (Table 3).

Since natural sounds often show irregularity in their pulse structures (e.g., erratic movements during feeding, flight, and stress), attention to this type of signal should be highly adaptive to any predator. Accordingly, it is not surprising that the most attractive sounds have irregular pulses (Myrberg et al. 1972, Nelson and Johnson 1972). Only two studies have compared the effects of natural and synthesized sounds. Nelson and Johnson (1970) believed that the sound produced by a "stampeded" school of bonefish (*Albula vulpes*) elicited slightly stronger response from their subjects than similarly structured synthesized sounds. In contrast, Banner (1972) showed that a synthesized sound possessing characteristics most conducive to attraction (i.e., rapid pulsing, low frequency, sufficient loudness) was generally as effective as natural sounds.

Unfortunately, we know little about the degree to which sharks recognize differences between extremely brief intervals within given sounds. Yet, there is no a priori reason why their ability should be less than the recognition afforded remarkably small intervals (less than 10 ms) by various teleosts

Table 3. Differential attraction of silky sharks to various instrumental signals, each having a different pulse character; all signals had the frequency spectrum of 25–50 Hz (Tongue of the Ocean, Bahamas).*

Sessions	Pulse nature of signal	No. of 3-min periods	No. of sightings of sharks[†]	Sightings per period ($\bar{x}$)
13 test sessions	Irregular	13	33	2.6
	10 Hz	13	24	1.8
	5 Hz	13	17	1.3
	1 Hz	13	14	1.0
13 control sessions	No signal	65	34	0.5
	Total		$\overline{122}$	

*From Myrberg et al. 1972.
[†]Distribution of sightings among the signals is significantly different from random distribution: -0.05 (Kolmogorov-Smirnoff, one sample test).

that have been recently examined (Ha 1973, Myrberg et al. in press, Spanier 1975). Probably temporal processing by the acoustical modality of fishes is an extremely sensitive and precise function.

Another important finding by Banner (1972) was that young lemon sharks do not respond to the specific nature of the source, i.e., prey versus nonprey; instead, differentiation rests upon the temporal characteristics of the sound, this being even more important than frequency composition. A similar conclusion was reached by others dealing with adult sharks (Myrberg et al. 1975, Richard 1968). Thus, this could not be attributed simply to the apparent inexperience of Banner's subjects. Since such sounds are commonly produced by prey (Banner, 1968, Hashimoto and Maniwa 1967, Moulton 1960, Nelson and Johnson 1970), the findings suggest that the rapid investigation of certain types of sounds results in enough opportunities for prey capture that appropriate responsiveness remains despite the fact that various types of nonprey sources produce similar sounds. Also, the effects of habituation on responsiveness in the absence of positive reinforcement indicate that energy would not be wasted for long in response to sounds produced by sources other than prey (see page 404).

Nelson and Johnson (1972) examined variation in pulse rate on acoustic attraction in four species of Pacific reef sharks (Fig. 2, Table 4). They found that low-frequency, pulsed sounds were more attractive if they had irregular rather than regular pulse intervals. No significant difference was found, however, between trains of pulses having equal duration and those having variable duration.

Sound Level—To be effective, a sound must be loud enough that subjects can hear it and orient to it. This factor is realistic only when ambient noise level is considered at the time of stimulation. The auditory
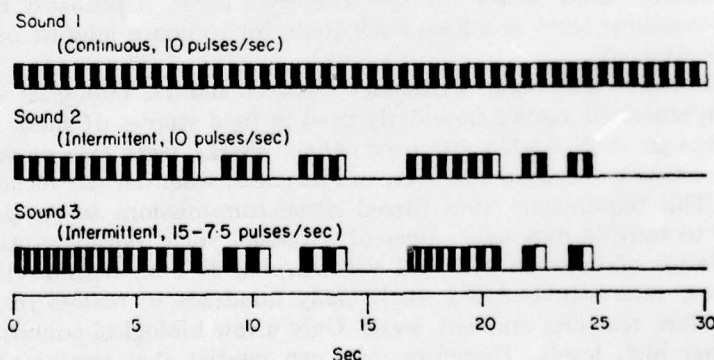

Figure 2 Diagrammatic representation of three 25- to 100-Hz pulsed sounds used for playback to sharks. The vertical black and white bars represent pulses (bursts of noise) but are not drawn to the absolute time scale. The 30-s sequences illustrated were repeated 10 times to comprise single 5-min playback periods. (Nelson and Johnson 1972)

Table 4. Number of sharks sighted and mean response intensities for three 25- to 100-Hz pulsed sounds. Based on 15 sound and 15 control periods for each sound (Eniwetok).*

Frequency	Number of sharks		Response intensity
	Sound	Control	
Sound 1, 10 Hz continuous	51	12	3.83
Sound 2, 10 Hz intermittent	102	18	5.25
Sound 3, 15 to 7.5 Hz, intermittent	100	14	5.50
Total	253	44	4.86[†]

*From Nelson and Johnson 1972.
[†]Mean of the maximum observed response intensities for each sound period; values based on an arbitrary eight-point scale.

sensitivity of fishes appears to be affected not only by prevailing ambient levels (Banner 1972, Buerkle 1968, Ha 1968, Tavolga 1967) but also by high ambient levels experienced prior to tesing (Ha 1968, Popper and Clarke 1976). Many workers have nevertheless neglected ambient noise as a potential source of disturbance. When responsiveness has been considered in sharks and teleosts, it often ceases when the signal level drops to a point between 15 and 25 dB above the prevailing spectrum-level ambient (e.g., Banner 1967, 1972; Buerkle 1969; Cahn et al. 1969; Myrberg et al. 1969; Nelson 1967). Thus, although a given signal may propagate quite far through the medium before falling below the spectrum-level noise, it probably reaches either an inaudible level or a level inadequate for response long before that distance is attained.

This illustrates one major difference between natural biological sounds and the synthesized signals frequently used in field studies of shark attraction. Although such studies occurred where sharks were rare or variable daily, an adequate sample size was, nevertheless, essential for meaningful analyses. This requirement thus forced signal transmissions to be at levels sufficient to provide reasonable areas of coverage. Such transmissions often attained levels of between +37 and +55 dB/μbar re 1 m. With a relatively smooth sea, such signals could reach many hundreds of meters from the sources before reaching ambient levels. Only a few biological sounds reach these rather high levels. Therefore, one can predict that most biological sounds of interest to sharks probably are detected only at distances much less than 100 m from the source.

An extreme example may be the maximum detection distances that Banner (1967) found for various prey sounds, using young lemon sharks in very shallow water ($\sim$30 cm depth). Such detection distances never exceeded

4.5 m for the prey sounds or 10 m for various synthesized sounds. These extremely short distances were understandable in this case because of the nature of the prey sounds used and the extreme attenuation of signal strength due to the extremely shallow water. These conditions allowed Banner to demonstrate, however, that the sharks responded by well-oriented approaches toward the sound source only when they were in an area in which the sound level exceeded that of previously established hearing thresholds of similar-sized animals under controlled laboratory conditions (see Fig. 3—measured in displacement values based on demonstrated sensitivity (Banner 1967)). Thus, at least in this case, directional responses appeared at the greatest detection distances. This differs somewhat from results of Chapman and Johnstone (1974) for the cod, in which the level required for directional responses in members of that species was higher than that necessary for detection. One reason for this difference may be the presence of a swim-bladder in the cod and its absence in sharks.

Qualities of a Sound that Appear Unimportant for Attraction

Within reasonable limits, certain features of underwater sounds are apparently not critical for attracting sharks. These include the duration of individual pulses within a given train of pulses (Nelson and Johnson 1972) and the summation, in time, of acoustic energy present in part or all of the pulse train (Myrberg et al. 1972). The latter study showed that silky sharks apparently find a signal with a train of 20 pulses/s, each pulse lasting 10 ms (i.e., 200 ms of energy), far more attractive than a signal of only 10 pulses/s, each pulse being 50 ms (i.e., 500 ms of energy). The latter, however, was far
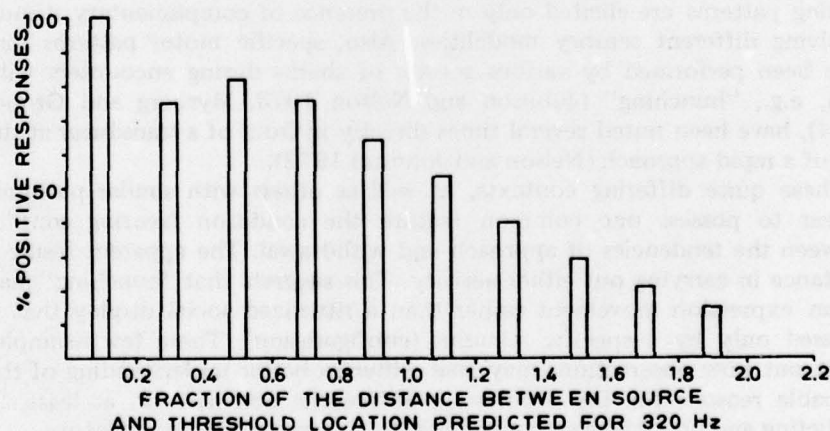

Figure 3 Percentages of positive responses by young lemon sharks at locations within and beyond the predicted threshold distance, the latter being calculated from displacement thresholds as measured in the laboratory for conspecifics of the same size. Results of attractive signals having optimum level at 320 Hz are combined. (Banner 1972)

more attractive than a third signal with 5 pulses/s, but whose pulses were
also 50 ms (i.e., 250 ms of energy).

Behavior of Sharks Subsequent to Attraction

As an ethologist, I am pleased that attraction studies have provided knowl-
edge in areas other than that concerned simply with the acoustical factors
underlying attraction per se. Acoustic attraction has provided an excellent
background for studying the behavioral activities of various species of sharks
in their natural environments; in most cases, the only environment where
that is possible, based on present inability to maintain the animals under
conditions appropriate for their health or for observation (Gruber and
Myrberg 1977; Myrberg, 1976). Although each field observation may be
brief, the knowledge gained over many periods can aid, for example, in
placing appropriate laboratory findings in reasonable perspective (Banner
1972, Evans and Gilbert 1971). Acoustic attraction also reduces dependence
on fortuitous encounters with sharks or on situations that often involve in-
tense feeding activities (e.g., when food is used to attract animals). Such
situations often result in rapid movements by sharks and preclude either
the observation or the occurrence of numerous behavior patterns exhibited
under less highly motivated conditions.

Although the behavioral activities noted during sonic attraction must be
associated with that context, such activities often relate to other contexts.
For example, the final approach to a loudspeaker may result in sharks
striking, biting, and even swallowing the entire apparatus (Banner 1968,
Myrberg et al. 1969, Nelson and Johnson 1972). This clearly suggests that
such animals need not perceive chemically or visually a familiar (food?)
object before attacking. This contrasts with earlier claims that complete
feeding patterns are elicited only in the presence of complimentary stimuli
involving different sensory modalities. Also, specific motor patterns that
have been performed by various species of sharks during encounters with
man, e.g., "hunching" (Johnson and Nelson 1973, Myrberg and Gruber
1974), have been noted several times directly in front of a transducer at the
end of a rapid approach (Nelson and Johnson 1972).

These quite differing contexts, as well as others with similar patterns,
appear to possess one common feature—the condition favoring conflict
between the tendencies of approach and withdrawal. The apparent result is
hesitance in carrying out either activity. This suggests that "hunching" may
be an expression movement rather than a ritualized social display that is
released only by a specific stimulus (configuration). These few examples
point out how observations may lead either to better understanding of the
probable reasons for the occurrence of specific activities or, at least, to
predicting and possibly even controlling the behavior of these predators.

Many species-typical action patterns by a variety of sharks have been ob-
served in the vicinity of a sound source. Many of these patterns have been
described by Myrberg and Gruber (1974); the rest are explained in the actual
accounts (Banner 1968, 1972; Myrberg et al. 1969, 1972, 1975*a*; Nelson and

Johnson 1970, 1972). The list of patterns includes those performed in apparent social contexts as well as others directed at the transducers themselves. The first group includes parallel swimming, circling, leaning, following, chasing, giving way, and hunching; the patterns of the second group include circling the transducer, veering off, hunching, biting, "startle," and head shaking. Patterns observed in either of these specific contexts include spinning, gill puffing, yawning, head shaking, and thrusting.

Given the same context, the strength of response appears to vary considerably among sharks (Limbaugh 1963). This has been shown clearly during sonic attraction. Nelson and Johnson (1972) found that the gray reef shark (*C. menisorrah*) approached an operating transducer more rapidly and more closely than did the reef whitetip (*Triaenodon obesus*).

The ultimate intensity of movements by sharks in a restricted area is often considered to be the feeding frenzy. Undoubtedly, this phenomenon is initiated and maintained partly by the social facilitation of movement by active sharks being close to one another. Such an effect has been noted in the vicinity of an active transducer that obviously provided an adequate stimulus situation. Relative speed of movement (Myrberg et al. 1969), intensity of approach (Nelson and Johnson 1972), and competitive feeding (Nelson et al. 1969) increase as sharks concentrate around a sound source. This suggests that the underlying motivation controlling the appropriate patterns of movement changes along a continuum and thus allows the energy used in specific activities to be adjusted to some level of apparent competition. Also, the number of sharks attracted to a source appears related to the number of sharks present within hearing range of the sound, at least during early trials (Banner 1972, Myrberg et al. 1975*a*, Nelson and Johnson 1972). This implies that attraction is effected regardless of motivational differences. Possibly a single common motivation underlies such responsiveness, but this is speculative. There is no a priori reason to believe, however, that motivation cannot change once a subject is close to the source. ·

Although hundreds of tests have been conducted on shark attraction there is a notable absence of reports on either intra- or interspecific aggression involving these animals, even when many are moving about in a relatively small area. This lack of obvious aggression has also been reported in various laboratory contexts (Myrberg and Gruber 1974). Yet at least some species—and probably all—possess a social organization apparently based on a dominant—subordinate system (Allee and Dickinson 1954, Clark 1963, Myrberg and Gruber 1974). Such an organization also crosses species lines (Cousteau and Cousteau 1970, Limbaugh 1963, Springer 1963, 1967). Although dominant—subordinate systems have been traditionally described and discussed within the context of aggression in other animal groups, the system as presently described in sharks might involve quite another context, i.e., predator—prey, the larger individual or the group being the potential predator and the smaller individual or the single animal within the group being the potential prey. Although there is some evidence militating against this idea (e.g., sexual differences—Myrberg and Gruber 1974), if that relationship is actually the basis for the apparent hierarchical organization in sharks, the continued use

of terms such as dominants and subordinates may be as relevant as applying such terms to cats and mice or foxes and rabbits. Future research will, it is hoped, bring added understanding to this problem.

The predatory nature of sharks relates well to their rapid response to sounds of wounded, struggling fishes. Yet, predation must surely extend beyond that limited source of food (Hobson 1963, Nelson et al. 1969). Banner (1968) hypothesized that hydroacoustic stimuli associated with normal feeding behavior in other fishes may also stimulate sharks to feed. This could be an even more significant stimulus than that from struggling prey. Such reasoning could explain why sharks are attracted to the natural sounds of prey and nonprey alike (Banner 1972). This leads to the inevitable conclusion that learning should play a role in the attraction process. Sharks have amply demonstrated not only that they are able to learn rapidly and retain a wide variety of tasks (e.g., Aronson et al. 1967, Graeber 1972, Graeber and Ebbesson 1972, Gruber and Schneiderman 1975) but also that individuals of different ages (based on size) within a given species often react quite differently in the same situation. For example, small members of many species are invariably more "curious," more "nervous," more unpredictable in their movements, and far less cautious than that noted in larger individuals (personal observation). This difference could be due to ontogenetic changes uninfluenced by experience, but under the conditions of relative food scarcity encountered by many, if not all, species of sharks, it would seem that the evolution of such carnivorous predators could ill afford food-related activities to be totally uninfluenced by experience.

One learning process commonly exhibited by sharks in the field is habituation to an attractive sound when trials are massed over a short period in the absence of reinforcement (Myrberg et al. 1969, Nelson et al. 1969) (Fig. 4). Nelson and Johnson (1972) suggested that this process might have affected daily variations in the results of their study. Myrberg et al. (1969) found, however, that at least in sharpnose sharks (*Rhizoprionodon* sp.—probably *R. porosus*), prehabituation levels of response to sounds reappeared approximately 1 hr after all sound transmission had stopped.

Such a learning process is apparent in other contexts as well. For example, Nelson and Johnson (1970) reported the following case: an 11-kg (25 lb) grouper had been speared but escaped deep into a hole where neither divers nor sharks could reach it. Within minutes, odors and sounds had attracted several reef whitetips that excitedly circled the site and explored the various holes leading to the fish. The sharks were unable to reach the wounded animal, and their excitement soon waned. Shortly, all disappeared. Chumming with fresh bait for the next hour at the site failed to attract a single shark. The probable importance of "learning to ignore" in these animals should not be regarded lightly by researchers, lest their hard-won data contain a sizable artifact.

The Antithesis of Approach—Withdrawal

An interesting and apparently paradoxical effect on the behavior of the few species of sharks examined thus far concerns the elicitation of a response
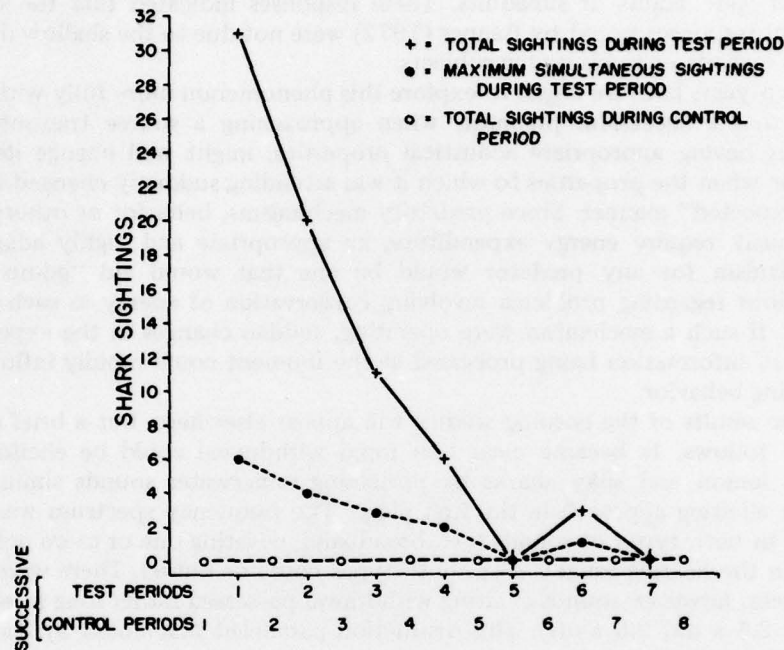
Figure 4 Decrease in sightings of sharpnose sharks, *Rhizoprionodon* sp., through successive test periods. Signals consisted of constant level, irregularly pulsed, overdriven 80 Hz sine waves (biphasic, symmetrical, and distorted square waves). Each test and control period—3 min. (Myrberg et al. 1969)

opposite to that of rapid approach, i.e., withdrawal—elicited by the use of sound. This unique pattern of response was reported by Banner (1972) during his bioacoustical study of young lemon sharks. His close attention to their behavior provided coherent clues as to probable causal relationships. Rapid flight appeared to occur at the precise moment certain sounds began. This was particularly true if sharks were approaching the source. Banner noted, however, that sounds consisting of closely spaced pulses rarely caused such responses. He thus hypothesized that during rapid approach, short intervals allowed the signal level to increase smoothly, which would not occur when a loud, impulsive sound, such as a single pulse or a signal possessing long intervals (seconds in length) was projected. Long intervals resulted in sudden jumps in level being experienced during an approach response. Only these two sound types, interestingly, elicited the so-called "startle" response in this study. As in the case of attraction, Banner found that these "startle" responses occurred only when the projected sound level at the location of "startle" was well above the established threshold sensitivity.

Strikingly similar withdrawal responses were first observed in silky sharks by our team in 1970 during a field study in the Tongue of the Ocean, Bahamas. Water depth was approximately 2000 m at the test site, and the

sharks were adults or subadults. These responses indicated that the withdrawal responses noted by Banner (1972) were not due to the shallow depth at his test site or to his young subjects.

Two years later we began to explore this phenomenon more fully with the idea that a successful predator, when approaching a source transmitting signals having appropriate acoustical properties, might well change its behavior when the properties to which it was attending suddenly changed in an "unexpected" manner. Since predatory mechanisms, behavior or otherwise, obviously require energy expenditure, an appropriate and highly adaptive mechanism for any predator would be one that would aid "go-no go" decisions regarding problems involving conservation of energy in such contexts. If such a mechanism were operating, sudden changes in the expected flow of information being processed at the moment could rapidly influence ongoing behavior.

The results of the ensuing studies will appear elsewhere, but a brief summary follows. It became clear that rapid withdrawal could be elicited in adult lemon and silky sharks by projecting underwater sounds similar to those eliciting approach in the first place. The frequency spectrum was the same in both types of sounds (i.e., broadband, covering one or more octaves within the hearing range). Also, both types could be pulsed. There were differences, however; sounds eliciting withdrawal possessed rather long intervals (e.g., 2.5 s on, 2.5 s off). This distinction paralleled that noted by Banner (1972).

An additional factor, mentioned by Banner as perhaps playing a role in the response, appeared to be most important. This concerned a sudden increase in the sound level as a subject approached the given source. For example, a sudden increase of 15 to 20 dB when a shark was within a few meters of the source resulted in the animal's retreating at a speed often faster than its initial approach. This response has been frequently documented from captive adult lemon sharks, held under conditions adequate for appropriate testing (Klimley 1976), as well as by young and adult free-ranging silky sharks found in the offshore waters of the Straits of Florida and the Tongue of the Ocean, Bahamas (Myrberg et al. 1975b). The basic response pattern was similar in both species; the restrictions imposed on the movements of the lemon sharks by the test facility (a large channel) resulted, however, in a more stereotyped form of withdrawal. Basically, this consisted of the shark moving in a reasonably narrow arc and proceeding in the direction from which it came. The pattern shown by silky sharks was more variable—probably due to the lack of any restrictions on their movements. The general response was neither a simple "startle" nor a series of rapid turns or sequences of apparently disorganized movements; rather, it consisted of a sequence of movements resulting in the animal(s) disappearing from view within 10 to 30 s of the change in the ongoing sound.

The orientation of such movements also showed that the animals recognized the direction of the sound source. Some individuals turned within a second or two of signal change through a narrow arc and headed out of visual range; others that had been heading directly at the transducer veered

off to the right or left and also headed out of view. These responses usually occurred when sharks were within 5 m of the source. Sharks farther from the source generally moved in a wide arc shortly after signal change, often disappearing from view in the direction from which they came. Although signal change was initiated when one shark had reached a distance of 5 to 10 m from the source, sharks farther away also reacted accordingly.

These sequences were especially clear for silky sharks approaching the transducer during withdrawal tests in the Straits of Florida. Silky sharks tested at specific locations in the Tongue of the Ocean exhibited greater variation in response. In the Straits, variations from the relatively rapid drift of our vessel during a given day of testing, the different drift tracks used each day, and the relatively few sharks seen on a given day substantially reduced any possible effects of habituation. In the Tongue of the Ocean, the same small population of silky sharks congregating around an offshore, deep-moored buoy was tested over a period of some hours. This provided the opportunity to determine possible changes in levels of responsiveness during repetitive testing. These data indicated that the "intensity" of withdrawal wanes if trials follow one another frequently. For example, if an appropriate sound is transmitted once every 5 to 10 min, rapid withdrawal is seen during the first two or three trials; less rapid withdrawal is elicited during the next few transmissions; finally, if the same sharks are attracted again within a few minutes, there will probably be little or no change in behavior when the supposed aversive stimulus is transmitted. Observers who have monitored both approach and withdrawal feel that withdrawal is more resistant to the effects of habituation, but this must be evaluated more precisely.

Clearly there are species differences in withdrawal response. Initial tests in the Tongue of the Ocean failed to bring about withdrawal in a small number of oceanic whitetip sharks (*C. longimanus*) under conditions that resulted in excellent withdrawal by silky sharks of similar or larger size. Although a more precisely monitored recent experiment showed that such responses could be elicited consistently at least two or three times by whitetips under nonfeeding conditions, much work remains before enough knowledge is gained to explain these species differences.

Finally, pure tones appeared quite ineffective in eliciting withdrawal, even at high levels. This fits closely the fact that such sounds are also not attractive to free-ranging sharks. This lack of response certainly implies an inability by these animals to hear pure tones, but this is not true based on laboratory findings using appropriate training techniques. This must mean that in the natural environment such tones have little or no meaning.

Various workers have tried to elicit withdrawal or avoidance responses from teleosts or, at least, to redirect their movements by using sounds. While a few have had varying degrees of success (e.g., Chapman 1976, Shiskova 1958, van Derwalker 1967), many have failed (e.g., Burner and Moore 1953, Miyake 1952, Moore and Newman 1956). Most reports mention initial startle responses to high-level, low-frequency sounds, but subjects apparently adjust rapidly to such sounds and return within moments to prior levels of activity. This again implies that such sounds have little aversive significance

for fishes, regardless of group. It may also mean, however, that the test animals were able to assess rapidly the relative value f specific stimuli in specific contexts. Thus, under the artificial conditions often present in "biological engineering" designs, fishes may well show no adaptive response because the context neither calls for it nor requires it. An appropriate context involving sounds of predators may well bring about unmistakable avoidance or withdrawal responses (e.g., Moulton 1960, Steinberg et al. 1965). Further study will surely expand on this point, but our findings with silky and lemon sharks suggest that appropriate sounds may indeed be aversive in the biologically adequate context.

Other workers mention similar withdrawal responses by sharks confronted by sudden sounds, such as yelling underwater (Eibl-Eibesfeldt and Hass 1959). Yet, there are also reports to the contrary (e.g., Hobson 1963). Although these differences may have been due to species differences or to variations in underlying motivation, possibly the latter case either involved sound levels below the hearing thresholds of the oncoming sharks or they did not cause a sufficient change in ongoing events to cause the animal to change course.

Apparently sound level per se cannot be the entire answer, since one sound at a given level will result in rapid withdrawal by sharks, while another at that same or even slightly higher level will attract them right up to the source. The real key to the problem may actually be the progressive increase in loudness as perceived by an approaching shark. Attraction may be initiated and maintained by moving toward a given sound whose level increases smoothly (relative to some unknown reference). Withdrawal, on the other hand, may be initiated and maintained by a sound whose structure results in sudden, increased levels, these levels differing greatly (relative to that same reference) from that just previously experienced (or expected) during approach. This implies that the shark is aware of a normal increase in level as it approaches the source. This formulation can be fitted into the well-known Biphasic Theory of approach/withdrawal processes as proposed by Schneirla (1959, 1965). Although the theory had originally been used to explain the organization of processes underlying early behavioral development in vertebrates, its author and others have subsequently attempted to apply it to other stages as well. The theory maintains that intensity of stimulation determines the operative process, i.e., approach or withdrawal. Undoubtedly, intensity plays an important role in attraction and withdrawal behavior in sharks but that factor per se seems less important than the nature of the increase in intensity during approach. The apparent importance for sharks of the latter factor suggests that its role should be evaluated in other groups of animals.

Directional Hearing

The rapid and directed orientation of free-ranging sharks to distant sound sources had been, until recently, the single exception to certain "rules" formulated by van Bergeijk (1964, 1967) in his popular theory of acoustic

orientation in fishes. In that theory, he maintained that (1) orientation to a sound source occurs only when a fish is extremely close to that source (i.e., within the acoustic near-field (see page 392) and (2) oriented responses are mediated only through the lateral line system, the labyrinths being precluded from that function.

This theory was of concern to naturalists and other functional biologists interested in the adaptive value of sound detection in fishes. Although it was clear that sharks and teleosts could detect low-frequency sounds, serious questions could be raised as to the importance of any such detection when sound sources had to be localized through random movement. Initial studies indicated that fishes followed the rules, the single exception being the sharks. Early tests of acoustic orientation in teleosts were invariably carried out under the acoustically complex conditions of the laboratory setting (for a critique, see Chapman and Hawkins 1973, Sand and Enger 1974). The only studies conducted in open waters were those centering on sharks, and these went counter to the rules. This suggested that some important factor or factors had been overlooked by van Bergeijk and subsequently by the adherents of his theory. If so, at least some teleosts might well also demonstrate far-field orientation under appropriate conditions.

These conditions were recently provided at various locations, with experiments being carried out at sea (Chapman 1973, Olsen 1969 *in* Sand and Enger 1974, Sand and Enger 1974, Schuijf 1974, Schuijf and Siemelink 1974, Schuijf et al. 1972) as well as in the laboratory (the latter using electrophysiological techniques—Enger et al. 1973, Sand 1974). These studies showed that selected teleosts can orient to sound in the far-field and in a number of instances that orientation is effected through the labyrinth organs.

Interest in spatial orientation has now shifted to the fascinating problem of its precise underlying mechanisms. Recently, Schuijf (1974) has proposed an elegant model to explain directional hearing in sharks and in teleosts without swimbladders. First, it states that directional hearing is not limited by distance, so long as the signal level exceeds the threshold for directional hearing at the existing noise level. Also, such animals can localize a sound source only if, in addition to the radial component of the particle displacement at the position of the fish, there is also a tangential component in the vertical plane through the source and the fish's position. The importance of the vertical plane to this model corresponds well with evidence that fishes are sensitive to displacements in both the horizontal and vertical planes.

The carefully reasoned theory certainly can explain instantaneous resolution of the 180° ambiguity within certain depth restraints. Once that ambiguity is resolved, even slight head movements of a moving shark should provide accurate information relative to a right-left decision if there is adequate detection by both ears and the respective axes of maximum sensitivity within the appropriate maculae are not parallel (see Vilstrup 1951, Figs. 16, 17, and 18). Differences in the amplitude of the *microphonic potentials* from the two labyrinths of the perch, *Perca fluviatilis*, have been shown to depend on the direction of vibration (Sand 1974; see discussion in Sand and Enger, 1974).

Another highly intriguing feature of hearing in sharks concerns those areas in the labyrinth that supply the information necessary for their demonstrated sensitivities and orienting abilities. Lowenstein and Roberts' (1951) study of the ear of the skate, *Raja clavata*, was for many years the only electrophysiological study of the elasmobranch labyrinth. Their findings demonstrated that low-frequency vibrations were adequate to elicit propagated discharges from the anterior portion of the saccular macula, a portion of the utricular macula (*lacinia utriculi*), and the macula neglecta. Vilstrup (1951), using lesion techniques, found acoustical sensitivity, however, only in the pars inferior of the spiny dogfish, *Squalus acanthias*. This was the state of the knowledge until only recently, when the macula neglecta, a little-known structure near the dorso-posterior aspect of the sacculus (Figure 5) came under study by Tester et al. (1972) and Fay et al. (1974). Because of its relative position and its high sensitivity to frequencies within the hearing range of sharks, it probably does detect sound. Electrophysiological experiments by Fay et al. (1974) on the blacktip reef shark, *C. melanopterus*, showed that the largest microphonic responses obtained from the macula neglecta
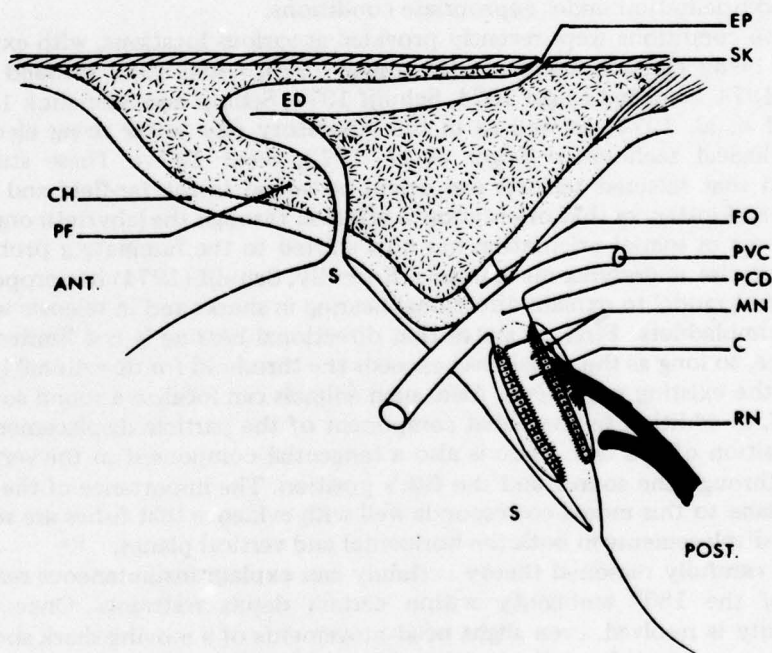

Figure 5 Schematic section of portions of the ear of the blacktip reef shark, *Carcharhinus melanopterus*. C. Cupula; CH, chondocranium; ED, endolymphatic duct; EP, endolymphatic pore; FO, fenestra ovalis; MN, macula neglecta; PCD, posterior canal duct; PVC, posterior vertical canal; PF, parietal fossa; RN, ramus neglectus nerve; S, sacculus; SK, skin covering fossa. (Fay et al. 1974)

were recorded when the parietal fossa was stimulated by slight vibrations, the response level falling rapidly as the stimulus was moved away from that location. They also found that the levels of response depended on the location of stimulation within the surface confines of the fossa. These findings, plus the remarkable similarity of various structures of the region (i.e., parietal fossa, the taut membranes of the fenestrum ovalis, the macula neglecta, and the latter's proximity to the sacculus and its associated endolymphatic duct) to the tympanic membrane and its associated structures in higher vertebrates cause one to question if this is merely coincidence. The obvious question is: why would a shark possess a tympanic-like membrane in its auditory system? Could the structure act like the swimbladder of teleosts, which transforms slight pressure fluctuations into appropriate displacements so as to increase sensitivity to far-field sound? The main difficulty is the absence of an apparent impedance discontinuity in the system. Could it be the seat of a nondirectional reference for the timing analysis, as required by Schuijf's model of directional hearing? The data strongly suggest that the maculae neglecta, lying directly below the membranes of the fenestra ovalis, are sensitive to particle motion (i.e., a velocity detector—Fay et al. 1974). Could that structural organization, centering on the macula neglecta, somehow impart directional information about a distant sound source? Further speculation is unjustified until more data confirm the system as part of the auditory system of sharks.

CONCLUSIONS

There can no longer be any doubt that sound plays an important role in the lives of sharks. It is used by them to locate food sources and possibly even other objects, such as competitors and predators. Results from studies using acoustical playback techniques have shown that repetitively pulsed, synthesized or naturally produced sounds, possessing frequency bands below 800 to 1000 Hz, are attractive to many species from a variety of habitats. Probably such sounds will eventually be found to be attractive to most, if not all, sharks. As one lowers the spectral content, attractiveness increases until an optimum is reached at very low frequencies, i.e., 40 Hz or below. Attractiveness increases also as repetitive pulsing increases (at least to 20 pulses/s), with irregular pulses being more effective than regular pulse trains. Pure tones and continuous sounds are not attractive to sharks.

Sharks perform a wide variety of behavioral activities in the vicinity of sound projectors. The technique of acoustic attraction therefore provides an opportunity to observe repeatedly various patterns of movements at times other than those of fortuitous encounters or when the animals have become highly excited by food used to attract them.

Under specific circumstances sounds can also elicit rapid withdrawal by sharks. Although much work remains to be done before this relationship can be described fully, it appears that some factor of intensity is central. There is evidence indicating that absolute intensity of sound is not the

critical point; rather, it is the manner whereby a given intensity is reached, i.e., rapidly or slowly, relative to some unknown reference. This area of research seems highly promising for reasons of biological interpretation and because of its general implications with regard to present theories of withdrawal processes in other animal groups.

The numerous theoretical and practical difficulties that have faced scientists during recent years regarding the problem of directional hearing in fishes seem now to have been alleviated, at least in part. There is presently good evidence that at least some teleosts and sharks do possess directional hearing, and as research proceeds the number of species demonstrating this ability will surely increase. Interest appears now to be shifting to the morphological and physiological mechanisms that impart directionality to hearing in these animals. There are a number of hypotheses and very few facts. Testing these and other ideas will be an important area of research for the next few years. Such research, it is hoped, will include sharks and other elasmobranchs among it subjects.

ACKNOWLEDGMENTS

REFERENCES

Allee. W. C., and J. C. Dickinson. 1954. Dominance and subordination in the smooth dogfish *Mustelus canis* (Mitchill). Physiol. Zool. 27:356-364.

Aronson, L. R., F. R. Aronson, and E. Clark. 1967. Instrumental conditioning and light-dark discrimination in young nurse sharks. Bull. Mar. Sci. 17(2):249-256.

Banner, A. 1967. Evidence of sensitivity to acoustic displacements in the lemon shark, *Negaprion brevirostris* (Poey). Pages 265-273 *in* P. Cahn, ed. Lateral line detectors. Indiana University Press, Bloomington, Ind.

Banner, A. 1968. Attraction of young lemon sharks, *Negaprion brevirostris*, by sound. Copeia. 4:871-872.

Banner, A. 1972. Use of sound in predation by young lemon sharks, *Negaprion brevirostris* (Poey). Bull. Mar. Sci. **22(2)**:251-283.

Bergeijk, W. A. van. 1964. Directional and nondirectional hearing in fish. Pages 281-299 *in* W. N. Tavolga, ed. Marine bio-acoustics. Pergamon Press, New York.

Bergeijk, W. A. van. 1967. The evolution of vertebrate hearing. Pages 1-49 *in* W. D. Neff, ed. Contributions to sensory physiology, vol. 2. Academic Press, New York.

Brown, T. 1968. Shark research programme at Rangiroa, French Polynesia, for the year 1968. Report to the French Polynesian Government.

Buerkle, U. 1968. Relation of pure tone thresholds to background noise level in the Atlantic cod (*Gadus morhua*). J. Fish. Res. Bd. Can. **25(6)**:1155-1160.

Buerkle, U. 1969. Auditory masking and the critical band in Atlantic cod (*Gadus morhua*). J. Fish. Res. Bd. Can. **26(5)**:1113-1119.

Burner, C. J., and H. L. Moore. 1953. Attempts to guide small fish with underwater sound. Spec. Sci. Rep., U.S. Fish & Wildlife Serv. **111**:33 pp.

Cahn, P. H., W. Siler, and J. Wodinsky 1969. Acoustico-lateralis system of fishes: tests of pressure and particle-velocity sensitivity in grunts, *Haemulon sciurus* and *Haemulon parrai*. J. Acoust. Soc. Amer. **46(6)**:1572–1578.

Chapman, C. J. 1973. Field studies of hearing in teleost fish. Helgolander wiss. Meeresunters. **24**:371-390.

Chapman, C. J. 1976. Some observations on the reactions of fish to sound. Pages 241-253 *in* A. Schuijf and A. D. Hawkins, eds. Sound reception in fish. Elsevier, New York.

Chapman, C. J., and A. D. Hawkins. 1973. A field study of hearing in the cod, *Gadus morhua* L. J. Comp. Physiol. **85**:147-167.

Chapman, C. J., and A. D. F. Johnstone. 1974. Some auditory discrimination experiments on marine fish. J. Exp. Biol. **61**:521-528.

Clark, E. 1963. The maintenance of sharks in captivity with a report on their instrumental conditioning. Pages 115-149 *in* P. Gilbert, ed. Sharks and survival. D. C. Heath and Co., Boston, Mass.

Cousteau, J. Y., and P. Cousteau. 1970. The shark—splendid savage of the sea. Doubleday, Garden City, N.J. 277 pp.

Derwalker, J. G. van. 1967. Response of salmonids to low frequency sound. Pages 45-58 *in* W. N. Tavolga, ed. Marine bio-acoustics, vol. 2. Pergamon Press, New York.

Eibl-Eibesfeldt, I., and H. Hass. 1959. Erfahrungen mit Haien. Z. Tierpsychol. **16(6)**:739-746.

Enger, P. S., A. D. Hawkins, O. Sand, and C. J. Chapman. 1973. Directional sensitivity of saccular microphonic potentials in the haddock. J. Exp. Biol. **59**:425-434.

Evans, W. E., and P. W. Gilbert. 1971. The force of bites by the silky shark (*Carcharhinus falciformis*) measured under field conditions. Naval Undersea

Research and Development Center, NUC TB 575, San Diego, Calif. 20 pp.

Fay, R. R., J. I. Kendall, A. N. Popper, and A. L. Tester. 1974. Vibration detection by the macula neglecta of sharks. Comp. Biochem. Physiol. 47A:1235-1240.

Graeber, R. C. 1972. Visual discrimination, learning, and central nervous system lesions in lemon (*Negaprion brevirostris*) and nurse sharks (*Ginglymostoma cirratum*). Ph.D. dissertation, University of Virginia, Charlottesville, Va.

Graeber, R. C., and S. O. E. Ebbesson. 1972. Visual discrimination learning in normal and tecta-ablated nurse sharks (*Ginglymostoma cirratum*). Comp. Biochem. Physiol. 42A:131-139.

Gruber, S. H. and A. A. Myrberg, Jr. 1977. Approaches to the study of the behavior of sharks. Amer. Zoologist.

Gruber, S. H., and N. Schneiderman. 1975. Classical conditioning of the nictitating membrane response of the lemon shark (*Negaprion brevirostris*). Behav. Res. Method and Instrum. 7(5):430-434.

Ha, S. J. 1968. Masking effects on the hearing of the lane snapper, *Lutjanus synagris* (Linnaeus). Master's thesis, University of Miami, Coral Gables, Fla. 51 pp.

Ha, S. J. 1973. Aspects of sound communication in the damselfish, *Eupomacentrus partitus*. Ph.D. dissertation, University of Miami, Coral Gables, Fla.

Hashimoto, T., and Y. Maniwa. 1967. Research on the luring of fish shoals by utilizing underwater acoustical equipment. Pages 93-104 *in* W. N. Tavolga, ed. Marine bio-acoustics, vol. 2. Pergamon Press, New York.

Hass, H. 1959. We come from the sea. Doubleday, Garden City, N.J. 288 pp.

Hobson, E. S. 1963. Feeding behavior in three species of sharks. Pacific Sci. 17:174-194.

Johnson, R. H., and D. R. Nelson. 1973. Agonistic display in the gray reef shark, *Carcharhinus menisorrah*, and its relationship to attacks on man. Copeia. (1):76-84.

Klimley, A. P. 1976. Analysis of sound stimuli eliciting withdrawal responses in the lemon shark, *Negaprion brevirostris* (Poey). Master's thesis, University of Miami Coral Gables, Fla.

Kritzler. H., and L. Wood. 1961. Provisional audiogram for the shark, *Carcharhinus leucas*. Sci. 133:1480-1482.

Limbaugh, C. 1963. Field notes on sharks. Pages 63-94 *in* P. W. Gilbert, ed. Sharks and survival. D. C. Heath and Co., Boston, Mass.

Lowenstein, O., and T. D. M. Roberts. 1951. The localization and analysis of the responses to vibration from the isolated elasmobranch labyrinth. A contribution to the problem of the evolution of hearing in vertebrates. J. Physiol. 114:471-489.

Miyake, I. 1952. Observations on sound production and response in tuna. Spec. Sci. Rep., U. S. Fish & Wildlife Serv. 91:59-68.

Moore, H. L., and H. W. Newman. 1956. Effects of sound waves on young salmon. Spec. Sci. Rep., U.S. Fish & Wildlife Serv. 172:1-19.

Moulton, J. M. 1960. Swimming sounds and the schooling of fishes. Biol. Bull. 119:210-223.

Myrberg, A. A., Jr. 1969. Attraction of free-ranging sharks by acoustic signals. Proc. Gulf Carib. Fish. Inst. 21st Annu. Sess., p. 135.

Myrberg, A. A., Jr. 1972. Using sound to influence the behavior of free-ranging marine animals. Pages 435-468 in H. E. Winn and B. L. Olla, eds. Behavior of marine animals—current perspectives in research, vol. 2. Plenum Press, New York.

Myrberg, A. A., Jr. 1976. Behavior of sharks—a continuing enigma. Nav. Res. Rev. 29(7):1-11.

Myrberg, A. A., Jr., and S. H. Gruber. 1974. The behavior of the bonnethead shark, *Sphyrna tiburo.* Copeia. (2):358-374.

Myrberg, A. A., Jr., A. Banner, and J. D. Richard. 1969. Shark attraction using a video-acoustic system. Mar. Biol. 2(3):264-276.

Myrberg, A. A., Jr., S. J. Ha, S. Walewski, and J. C. Banbury. 1972. Effectiveness of acoustic signals in attracting epipelagic sharks to an underwater sound source. Bull. Mar. Sci. 22(4):92-94.

Myrberg, A. A., Jr., C. R. Gordon, and A. P. Klimley. 1975a. Attraction of free-ranging sharks by acoustic signals in the near-subsonic range. Tech. Rept. to Office of Nav. Res., Contract No. N00014-67-A-0201-0008. Rosenstiel School of Marine and Atmospheric Science, TR75-4, University of Miami, Coral Gables, Fla. 42 pp.

Myrberg, A. A., Jr., C. R. Gordon, and A. P. Klimley. 1975b. Rapid withdrawal from a sound source by sharks under open-ocean and captive conditions. Tech. Rept. to Office of Nav. Res., Contract No. N00014-67-A-0201-0008. Rosenstiel School of Marine and Atmospheric Science, TR75-5, University of Miami, Coral Gables, Fla. 32 pp.

Myrberg, A. A., Jr., C. R. Gordon, and A. P. Klimley. 1976. Attraction of free ranging sharks to low frequency sound, with comments on its biological significance. Pages 205-228 in A. Schuijf and A. D. Hawkins, eds. Sound reception in fishes. Elsevier, New York.

Myrberg, A. A., Jr., E. Spanier, and S. Ha. In press. Temporal patterning in acoustical communication. *In* E. S. Reese, ed. Contrasts in behavior. Wiley and Sons, New York.

Nelson, D. R. 1967. Hearing thresholds, frequency discrimination, and acoustic orientation in the lemon shark, *Negaprion brevirostris* (Poey). Bull. Mar. Sci. 17(3):741-768.

Nelson, D. R., and S. H. Gruber. 1963. Sharks: attraction by low-frequency sounds. Sci. 142(3594):975-977.

Nelson, D. R., and R. H. Johnson. 1970. Acoustic studies on sharks, Rangiroa Atoll, July 1969. Tech. Rept. to Office of Nav. Res., Contract No. N00014-C-0318. Long Beach Calif. State College Found. Rept. No. 2, 15 pp.

Nelson, D. R., and R. H. Johnson. 1972. Acoustic attraction by Pacific reef sharks: effects of pulse intermittency and variability. J. Comp. Biochem. Physiol. 42A:85-95.

Nelson, D. R.. R. H. Johnson, and L. G. Waldrop. 1969. Responses in Bahamian sharks and groupers to low frequency, pulsed sounds. Bull. S. Calif. Acad. Sci. **68(3)**:131-137.

Olla, B. 1962. The perception of sound in small hammerhead sharks, *Sphyrna lewini*. Master's thesis, University of Hawaii, Honolulu, Hawaii.

Popper, A. N , and N. L. Clarke. 1976. The auditory system of the goldfish *Carassius auratus*: effects of intense acoustic stimulation. Comp. Biochem. Physiol. **53A**:11-18.

Richard, J. D. 1968. Fish attracted with pulsed low-frequency sound. J. Fish. Res. Bd. Can. **25(7)**:1441-1452.

Sand, O. 1974. Directional sensitivity of microphonic potentials from the perch ear. J. Exp. Biol. **60**:881-899.

Sand, O. and P. S. Enger. 1974. Possible mechanisms for directional hearing and pitch discrimination in fish. Rheinisch-Westfälische Akad. d. Wissenschaft, 53(Symposium-Mechanoreception):223-242.

Schneirla, T. C. 1959. An evolutionary and developmental theory of biphasic processes underlying approach and withdrawal. Pages 1-42 *in* M. R. Jones, ed. Current theory and research on motivation, vol. 7. University of Nebraska Press, Lincoln, Nebr.

Schneirla, T. C. 1965. Aspects of stimulation and organization in approach/withdrawal processes underlying vertebrate behavioral development. Pages 1-74 *in* R. Hinde, D. Lehrman, and E. Shaw, eds. Advances in the study of behavior. University of Nebraska Press, Lincoln, Nebr.

Schuijf, A. 1974. Field studies of directional hearing in marine teleosts. Ph.D. dissertation, University of Utrecht, Netherlands.

Schuijf, A., and M. E. Siemelink. 1974. The ability of cod (*Gadus morhua*) to orient towards a sound source. Experientia **30**:773-774.

Schuijf, A., J. W. Baretta, and J. T. Wildschut. 1972. A field investigation on the discrimination of sound directon in *Labrus berggylta* (Pisces: Perciformes). Neth. J. Zool. **22**:81-104.

Shiskova, E. V. 1958. Concerning the reactions of fish to sounds and the spectrum of trawler noise. Rybnoe Khozyaistvo. **34(3)**:33-39.

Spanier, E. 1975. Sound recognition by damselfishes of the genus *Eupomacentrus* from Florida waters. Ph.D. dissertation, University of Miami, Coral Gables, Fla.

Springer, S. 1963. Field observations on large sharks of the Florida-Caribbean region. Pages 95-113 *in* P. W. Gilbert, ed. Sharks and survival. D. C. Heath and Co., Boston, Mass.

Springer, S. 1967. Social organization of shark populations. Pages 149-174 *in* P. W. Gilbert, R. F. Mathewson, and D. Rall, eds. Sharks, skates, and rays. Johns Hopkins Press, Baltimore, Md.

Steinberg, J. C., W. C. Cummings, B. D. Brahy. and J. Y. MacBain (Spires) 1965. Further bio-acoustic studies off the west coast of North Bimini, Bahamas. Bull. Mar. Sci. **15(4)**:942-963.

Tavolga, W. N. 1967. Masked auditory thresholds in teleost fishes. Pages 233-243 *in* W. N. Tavolga, ed. Marine bio-acoustics, vol. 2. Pergamon Press, New York.

Tester, A. L., J. I. Kendall, and W. B. Milisen. 1972. Morphology of the ear of the shark genus *Carcharhinus* with particular reference to the macula neglecta. Pacific Sci. 26(3):264-274.

Vilstrup, T. 1951. Structure and function of the membranous sacs of the labyrinth in *Acanthias vulgaris*. Ejnar Munksgaard, Copenhagen. 134 pp.

Wisby, W. J., and D. R. Nelson. 1964. Airplane observations of acoustic orientation in sharks. Amer. Fish. Soc. Conf. (Abstr.).

Wisby, W. J., J. D. Richard, D. R. Nelson, and S. H. Gruber. 1964. Sound perception in elasmobranchs. Pages 255-268 *in* W. N. Tavolga, ed. Marine bio-acoustics. Pergamon Press, New York.

Wright, B. 1948. Releasers of attack behavior patterns in shark and barracuda. J. Wildlife Manage. 12(2):117-123.

ACOUSTIC STIMULI UNDERLYING WITHDRAWAL FROM A SOUND SOURCE BY ADULT LEMON SHARKS, *NEGAPRION BREVIROSTRIS* (POEY)

A. PETER KLIMLEY AND ARTHUR A. MYRBERG, JR.

ACOUSTIC STIMULI UNDERLYING WITHDRAWAL FROM A SOUND SOURCE BY ADULT LEMON SHARKS, *NEGAPRION BREVIROSTRIS* (POEY)

A. Peter Klimley and Arthur A. Myrberg, Jr.

ABSTRACT

The acoustical factors responsible for eliciting withdrawal (180° turn and departure) from the vicinity of a sound source by adult lemon sharks were investigated. Four sounds were examined on separate days: (1) killer whale scream, (2) 500 to 4,000 Hz noise-band (same bandwidth as the scream), (3) 500 Hz pure tone, and (4) 150–300 Hz pulsed noise-band. While the scream elicited more withdrawals than the pulsed noise-band and pure tone at similar sound pressure levels, it elicited fewer responses than the continuous noise-band. The latter result was also obtained when the scream and the continuous noise-band were played back (in alternation) on the same day. The relative effectiveness of these various sounds in eliciting withdrawal, thus, does not stem only from a species-specific recognition of a predator's call. Although sharks continued to approach the source of the 150 to 300 Hz pulsed noise-band when small incremental changes were made in sound pressure levels, withdrawal was elicited when increases involved considerable change. This suggested that withdrawal was based on stimulus magnitude and/or rate of level rise. Sharks were then exposed to one rate of increase (96 dB/sec) at several magnitudes above broad-band ambient level (3, 6, 9, 12, 15, 18 dB) and several rates (6, 24, 96 dB/sec) at one magnitude (18 dB). Findings showed that withdrawal depended upon both the magnitude and rate of increase in level of the stimulus. Trials during a given day did not affect the occurrence of withdrawal on successive days. A decrease in response was noted when water temperature dropped below 21°C.

Recent studies have demonstrated that sharks are attracted to sounds that possess specific acoustical properties. These properties include low frequency (Myrberg et al. 1969; 1972; Nelson and Gruber, 1963), broad bandwidth (Myrberg et al. 1969), and amplitude modulation (Myrberg et al. 1972; Nelson and Gruber, 1963). As frequency decreases, or pulse rate increases, attraction is augmented (Myrberg et al. 1972). Furthermore, irregularly pulsed sounds are more effective attractants than regularly pulsed sounds (Myrberg et al. 1972; Nelson and Johnson, 1972).

Sounds also evoke withdrawal from sharks. Eibl-Eibesfeldt and Hass (1959), as well as Nelson (1969), noted that reef sharks are repelled by shouts. A confounding variable, however, in both cases was the presence of abrupt body movements. Hobson (1963), on the other hand, found shouts ineffective at putting different species of reef sharks to flight, as did Hass (1973) when dealing with the oceanic whitetip, *Carcharhinus longimanus*, the tiger shark, *Galeocerdo cuvieri*, and the white shark, *Carcharodon carcharias*. Banner (1972) noted that juvenile lemon sharks fled at the onset of a sound if they had moved rapidly to a position where the intensity of the sound was well above their hearing thresholds. Such was also noted for adult silky sharks, *Carcharhinus falciformis*, by Myrberg et al. (1975). Brown (1973) observed withdrawal by five species of sharks from sources emitting either broad-band sounds or combinations of pure tones whose frequencies were above those effective in attraction (frequencies not indicated) and below 7,000 Hz (this finding does stand in contrast, however, with the repeated absence of any response at similar frequencies in studies of hearing sensitivity among a variety of sharks, e.g., Banner, 1972; Kelly and Nelson, 1975; Kritzler and Wood, 1961; Nelson, 1967a; Olla, 1962).
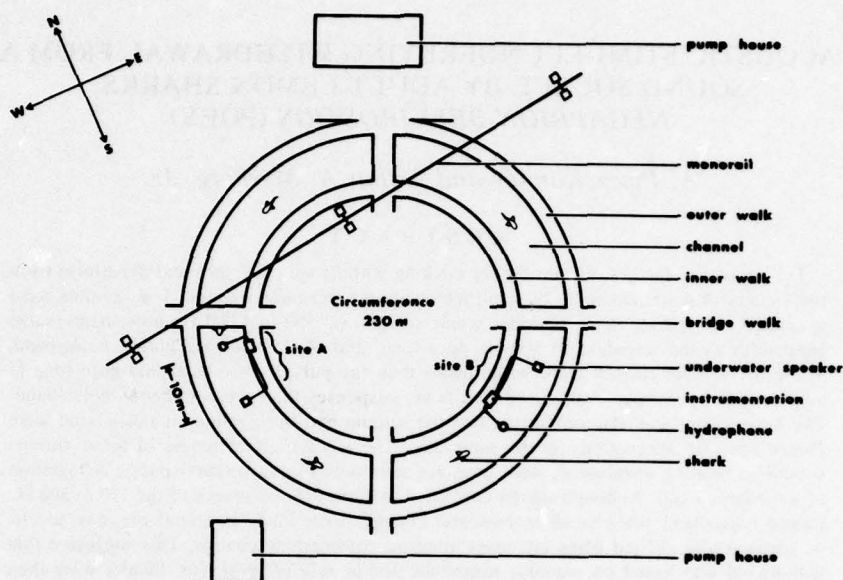
Figure 1.   Shark Channel exhibit and testing sites.

Our experiments were conducted to determine whether or not adult lemon sharks, *Negaprion brevirostris,* would withdraw from specific types of sound and, if so, to establish those factors crucial for such a response.

METHODS AND MATERIALS

Experiments were conducted in the concrete Shark Channel exhibit of the Miami Seaquarium. This circular channel has an outer circumference of 230 m, width of 7 m, and depth of 1.6 m. Several cm of sediment cover the bottom. Two different test sites, A and B (Fig. 1), were chosen because sharks consistently swam through both areas without reversing direction and testing at these particular sites did not prevent patrons from viewing the sharks.

Although the acoustical conditions of the channel were not ideal, they were compatible with the aims of our study. Also the size of the channel provided the opportunity to conduct appropriate tests using large, freely moving sharks, at a level of precision unobtainable under open-field conditions.

Acoustical Considerations

Throughout the study sound pressure level (SPL) measurements were made of the test sounds. Measurements of particle velocity were not performed due to the Seaquarium management's insistence that a device holding an accelerometer not be mounted in the channel. It has been shown that lemon sharks respond to particle motion rather than sound pressure (Banner, 1967; 1972). Although Banner (1971) had previously found that velocity/pressure signal ratios were similar at all distances tested (24 m maximum) from a speaker in an extremely shallow bay (depth ~ 60 cm), we could not assume such a relationship in our arena. However, since increases in SPL were paralleled by increases in responsiveness throughout the study (see below), it is likely that the measured sound pressures were proportional to the acoustic factor to which the sharks were attending. Sounds were generated throughout the early phases of the study from a cassette tape recorder (Panasonic, RQ-309S). The output signal, gated by a toggle switch, passed through an attenuator (Hewlett Packard, 350D) and then entered a power amplifier (Allen Organ, T-50, 40 w), its output monitored with a RMS voltmeter (Hewlett Packard, 400GL). The toggle switch initiated playback, and the attenuator controlled the signal level. Sounds were transmitted by an underwater speaker (Dyna, J-9), positioned in the center of the shark channel, on the bottom.

Playback System

noise generator → band pass filter → linear level increase → pre-ampl. 20dB

cassette tape recorder → attenuator → power amplifier → R.M.S. voltmeter

sound projector

Recording System

pre-ampl. 40dB → oscilloscope

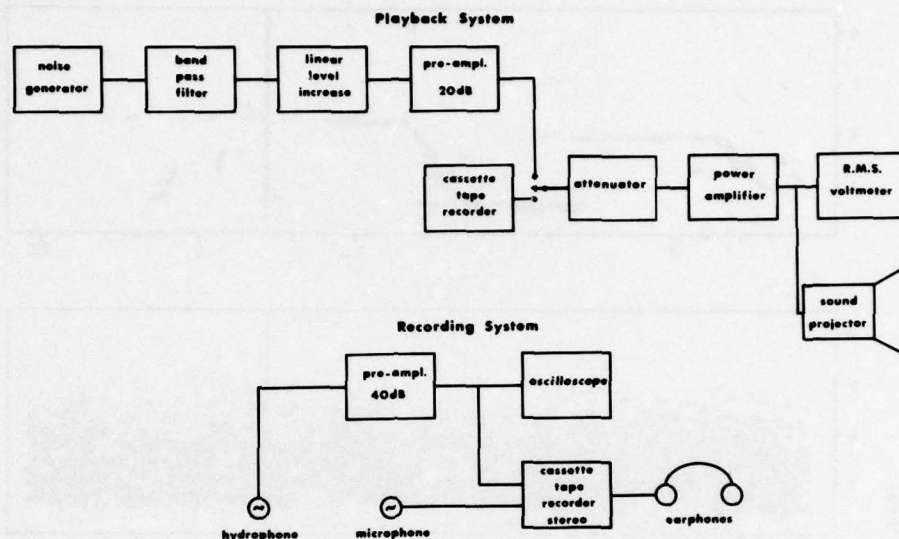hydrophone   microphone → cassette tape recorder stereo → earphones

Figure 2.   Block diagram of instrumentation.

The recording system included a hydrophone (Clevite, CH17M) in line with a preamplifier (Ithaco, 144L, 40 dB gain), an oscilloscope (Tektronix, 323), and a two-channel cassette recorder (Superscope, CD301). The test signal was recorded on one channel of the recorder, narrative on the other. Headphones and the oscilloscope allowed monitoring during playback. The instrumentation used during the study is shown in Figure 2.

Investigators of hearing sensitivity in fishes have noted great variation in SPL at different locations within testing enclosures with a single frequency (Cummings et al. 1975; Hawkins and MacLennan, 1976; Nelson, 1967a; Tavolga and Wodinsky, 1963) as well as at a single location with different frequencies (Cummings et al. 1975; Hawkins, 1973). This variation has been attributed to constructive and destructive interference of sound, reflected from the enclosure walls and water surface (Cummings et al. 1975; Hawkins, 1973; Parvulescu, 1964). For these reasons, stimulus variation within the channel was mapped before testing began.

Measurements of ambient noise were made at a distance of 10 m from the speaker at sites A and B. Readings of total SPL (= broad-band) and spectrum levels at 250, 500, 1,000, 2,000, and 4,000 Hz were taken at 1 m intervals across the channel at mid depth (80 cm). At distances of 2 and 4 m from the inner boundary of the channel, broad-band measurements were also performed at two additional depths (40 and 120 cm). Three consective series of measurements were performed in all cases.

The mean ambient spectrum levels from both sites (250 Hz, 75 dB/μPa; 500 Hz, 71 dB/μPa; 1,000 Hz, 68 dB/μPa; 2,000 Hz, 60 dB/μPa; 4,000 Hz, 51 dB/μPa) were slightly higher than those found by Wenz (1962, p. 1952, fig. 13) for low sea state and high mechanical (i.e., heavy traffic) noise. The mean, broad-band ambient level was similarly high (105 dB/μPa). Such high levels were probably due to nearby sound sources such as a monorail, filter pumps, and a public address system.

Although the mean ambient spectrum levels differed by about 2 dB across the channel at both sites, the broad-band ambient measurements at site A differed by 9 dB and at site B by 7 dB. At both sites broad-band ambient differed by about 2 dB with depth. By restricting future testing to the center portion of the channel, 1.5 m from either boundary, variation was reduced to only 3 dB.

Hourly measurements of broad-band ambient noise were made at mid depth at the center of the channel from 0800 to 2200 h to determine those times with the most stable noise level. Differences of only 2 dB occurred during the selected test periods, i.e., 0800 to 1200 and 1800 to 2200 h.

Spectrum level measurements of a transmitted band of 500 to 4,000 Hz pink noise were made at site A (excluding 250 Hz). Variation in spectrum level across the channel was greater at lower frequencies (7 dB at 500 Hz, 4 dB at 1,000 Hz, 2 dB at 2,000 Hz, and 1 dB at 4,000 Hz). By restricting tests to the central region of the channel (1.5 m from each boundary), variation at 500 and 1,000 Hz was reduced to 4 and 3 dB, respectively. Broad-band level during playback of the same sound varied 7 dB across the channel. By similarly restricting tests to the region mentioned above, that variation was reduced to 3 dB.
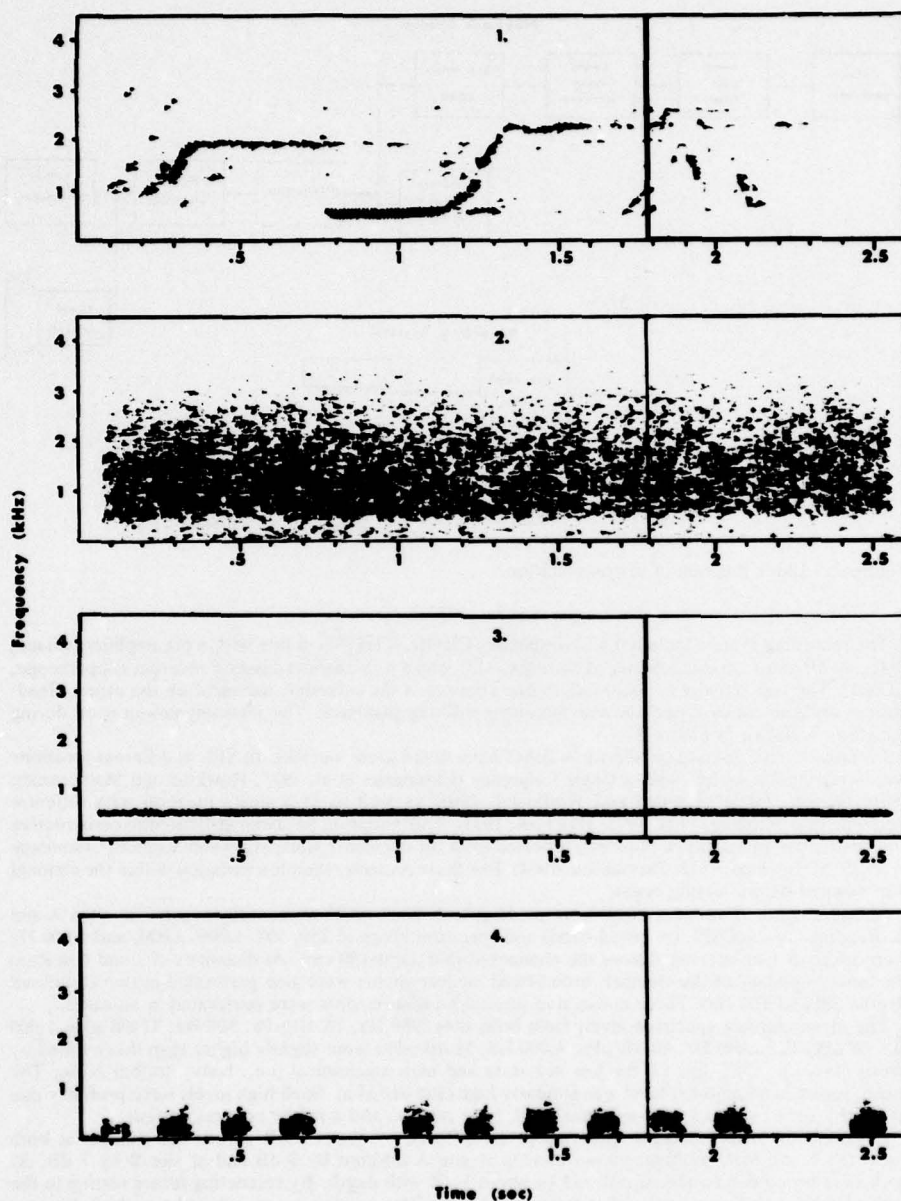
Figure 3.   Spectrograms of sounds played back to lemon sharks: (1) killer whale scream, (2) 500 to 4,000 Hz noise-band, (3) 500 Hz pure tone, and (4) 150 to 300 Hz pulsed noise-band.

Additional broad-band measurements of the transmitted noise-band were taken at distances of 10, 20, and 40 m in both directions from the speaker to measure transmission loss. Measurements were also attempted 80 m from the speaker; however, the signal could not be detected above ambient levels at that distance. The signal attenuated at a mean of 9 dB per distance doubling.

The Test Sounds

Playbacks of killer whale calls have elicited flight by whales (*Delphinapterus leucas*—Fish and Vania, 1971; *Eschrichtius robustus*—Cummings and Thompson, 1971) and penguins (*Spheniscus demersus*—Frost et al. 1975). The latter two authors noted whales and penguins are prey of the killer whale and concluded this response to be antipredatory in nature. Sharks are also occasional prey of the killer whale (Cousteau and Cousteau, 1970; Martinez and Klinghammer, 1970). To test whether their responsiveness to sounds might be a specific predator-avoidance stratagem, the killer whale scream (Schevill and Watkins, 1966, for description) was included among the sounds played back to the lemon sharks. This particular type of sound had previously elicited flight responses from grey whales (William Cummings, pers. comm.).

Three other sounds were transmitted into the channel: (1) a continuous band of 500 to 4,000 Hz pink noise [slope emphasized lower frequencies], (2) a 500 Hz pure tone, and (3) a pulsed band of 150 to 300 Hz pink noise [5 pulses/sec., pulse duration of 100 m/sec]. The sounds had been recorded at about the same level as that of the scream and possessed the same 2.5 sec. envelope. The noise-band contained all the frequencies of the scream but it lacked the characteristic frequency and amplitude modulation. The pure tone matched the dominant low-frequency component of the scream; the dominant high-frequency component was not included since it lies beyond the hearing range of the lemon shark (Nelson, 1967a; Banner, 1972). The pulsed noise band was identical to that which had elicited rapid approach responses in carcharhinid sharks (Myrberg et al. 1969). All sounds were recorded on 30 min cassettes, each 2.5 sec of signal being separated by 2.4 sec of silence. Sound spectrograms of all four sounds are given in Fig. 3.

Experimental Design

Signals were transmitted, either at site A or B, whenever a shark reached 10 m from the underwater speaker, and a response was only scored if it occurred between 9 and 10 m from the sound projector. Ten m was chosen to reduce the likelihood that response would be mediated by viewing the speaker. If a withdrawal response (a reverse in direction of swimming) was observed at a particular SPL, the shark was followed to see whether it responded similarly in the absence of the signal the next time it moved through the same area. The effectiveness of transmission was established by comparing the number of responses recorded during tests to the number recorded during control periods (i.e., when signals were not transmitted).

During a test period, the SPL of the signal was increased above broad-band ambient by 3 dB steps if the sharks did not withdraw; it was not increased if the sharks withdrew. If six consecutive withdrawals were observed, testing was discontinued for that day. The magnitude of the signal during playback was expressed as the level, in dB, above the ambient noise level since Nelson (1967b) found in lemon sharks that unconditioned responses to intense sound stimuli were determined by sound amplitude relative to background noise (random noise being used to change the level of background).

One test signal was played back in the ascending manner every third day from 0800 to 1200 h. Three series of all four test signals were run during April, July, August, and September. The mean number of consecutive responses at each sound level was calculated for each signal.

Seven adult sharks served as subjects: four males, 1.5 to 2.5 m total length, and three females, 2.0 to 2.5 m total length. All had been captured shortly before testing began. Each was identified by length and fin irregularities. The animals were fed three times daily during public feedings. All appeared in good health except for occasional patches of ectoparasites in the late spring and wounds on the leading edge of the dorsal fins of the largest male and female.

Nelson and Johnson (1972) suspected long-term habituation to sounds used in attracting reef sharks. This was based on a reduction over several days of the numbers of sharks attracted to a speaker and a lessening of the sharks' responsiveness to sound. Myrberg et al. (1969), on the other hand, did not observe habituation of sharks attracted in three-min playback-periods separated by more than an hour. Preliminary playback-tests were therefore conducted with one signal repeated at three different time intervals (96, 48, and 24 h). Similarity of response, regardless of interval, indicated that there was no habituation to signals separated by intervals of 24 h or more.

Short-term habituation to signal presentations separated by less than 24 h was also considered. Nelson (1967b) found slight habituation of bradycardia in sharks to sounds of high amplitude during repetitive presentations over a day of testing while Myrberg et al. (1969) and Nelson (1969) noted habituation of attraction responses over consecutive 3- and 15-min playback-periods, respectively. The sharks in our study usually moved separately through the channel at speeds such that a minimum of 15 min separated each test (i.e., playback and control). This procedural point prevented sufficient testing of any short-term habituation. Such tests were therefore deferred to the open ocean where relatively rapid repetitive presentations could be achieved based on the large number of sharks at-
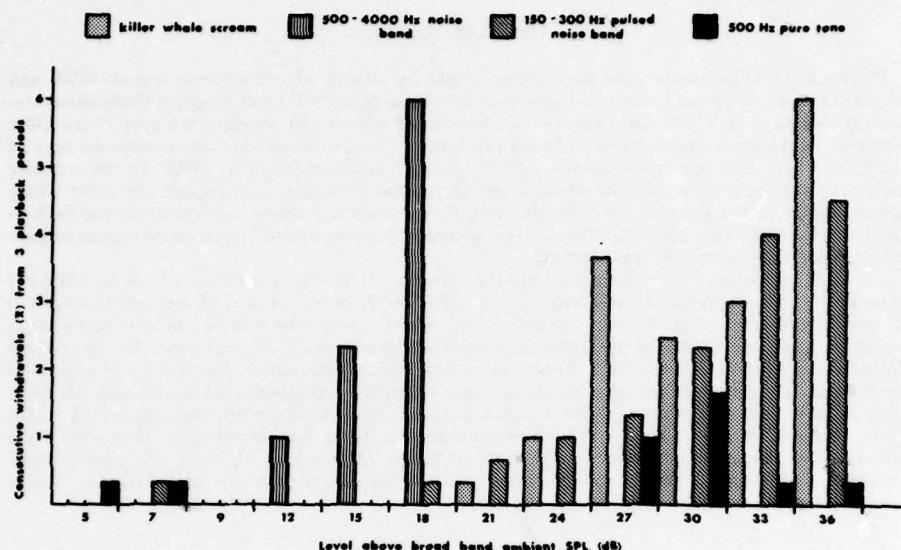
Figure 4.   Mean consecutive responses of sharks at ascending levels above broad-band ambient SPL for four test sounds. Playback of sounds on a single day were discontinued if six consecutive responses were observed.

tracted to a sound source. This phenomenon has subsequently been demonstrated in silky sharks (Myrberg et al. 1978).

An additional experiment determined whether the response differentials obtained in the previous experiment might have been associated with slightly different ambient noise conditions on different days. To control for this, the scream and the 500 to 4,000 Hz noise-band were randomly played back on the same day to sharks at the same level, i.e., 18 dB above the broad-band ambient noise level.

RESULTS

The relative effectiveness of the four signals in eliciting withdrawal responses can be seen in Figure 4. Means of responses during all three playback periods for each of the four test signals are given at different, ascending SPLs above broad-band ambient (105 dB/μPa). A mean of one response was reached at 24 dB for the scream while a mean of six consecutive responses for the same sound was reached at 36 dB. Responses to the 500 to 4,000 Hz noise-band reached a mean of one at 12 dB and a mean of six responses at 18 dB. The pure tone attained a response mean of one at 27 dB but only reached a maximum mean of 1.6 at 30 dB. The pulsed 150 to 300 Hz noise-band reached a mean of one at 24 dB and a maximum mean of 4.5 at 36 dB.

Significant differences were found between the number of withdrawals shown to each sound and that shown in its absence: (1) a difference existed between the 31 responses [56 playbacks] during the scream and the four responses [43 controls] in its absence [χ^2, Yate's Cor., df = 1, $P < 0.001$], (2) 28 resps. [46 playbacks] for the noise-band versus four resps. [43 controls] during its absence [$P < 0.001$], (3) 31 resps. [70 playbacks] for the pulsed noise-band versus five resps. [44 controls] during its absence [$P < 0.001$], and (4) 11 resps. [50 playbacks] for the pure tone versus 1 resp. [40 controls] during its absence [$P < 0.001$].

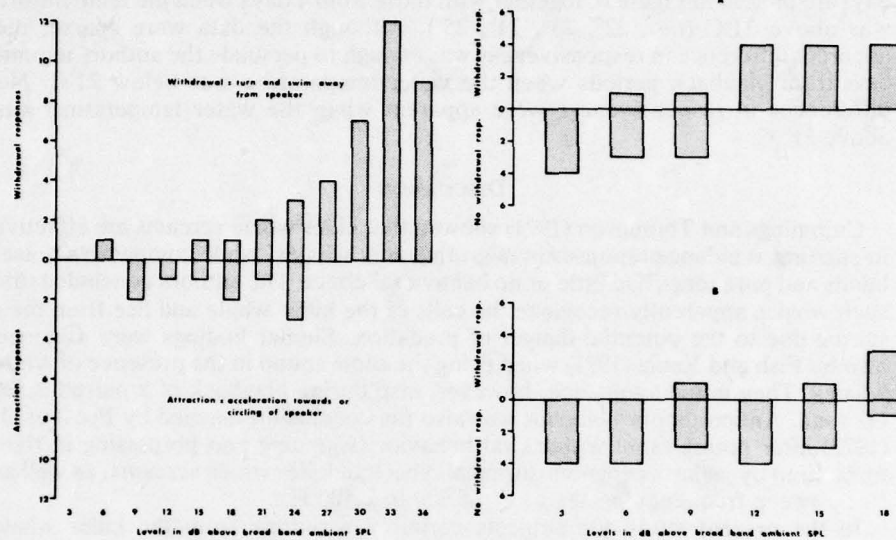Although withdrawals increased in occurrence with increasing stimulus mag-

Figure 5.   Attraction and withdrawal responses to pulsed noise at ascending levels above broad-band ambient.

Figure 6.   Withdrawal responses to signals at ascending levels above broad-band ambient SPL during four playback periods when temperatures in the channel were (A) above 21°C and (B) below 21°C.

nitude of the scream and the noise-bands, such was clearly not the case with the pure tone. Perhaps the explanation for the absence of this relationship lies in the relatively insensitivity of the sharks to such a stimulus, barely propagated at response threshold. At this level, the responses may then have occurred sporadically due to the ±3 dB SPL variation in stimulus intensity due to the shark's location in the channel at signal onset.

The superior effectiveness of the 500 to 4,000 Hz noise-band over that of the killer whale scream was corroborated when the two signals were played back at a level 18 dB above broad-band ambient on the same day. Out of 20 playbacks of each signal, the sharks withdrew from the noise-band 16 times while withdrawing from the scream only four times (χ^2, Yate's Cor., $P < 0.02$).

Withdrawal from the pulsed noise-band was of particular interest since in bandwidth and pulse characteristics it was similar to signals that had attracted sharks in a previous study (Myrberg et al. 1969). Indeed, sharks were likewise attracted to the transducer at low stimulus intensities (9 to 24 dB) (Fig. 5). They altered their swimming path, veering laterally and descending in depth toward the speaker. Often this was accompanied by a slow glide, tail movements ceasing at the time. In several cases the sharks circled the speaker before returning to the surface and proceeding in the same direction as they had been moving. However, at higher stimulus intensities (27 to 36 dB) the sharks withdrew from the vicinity of the transducer (Fig. 5). The switch from attraction to withdrawal at increasing SPLs implied that the magnitude of the stimulus and/or rate of its increase are important factors in the evocation of withdrawal.

The water temperature in the channel fell below 21°C during four playback periods. The response data from these 4 days (20°C on 3 days and 19°C on 1

day) are plotted in Figure 6, together with those from 4 days when the temperature was above 21°C (i.e., 22°, 23°, 24°, 25°). Although the data were sparse, the apparent difference in responsiveness was enough to persuade the authors to omit data from playback periods when the water temperature was below 21°C. No differences in responsiveness were apparent when the water temperature was above 21° C.

DISCUSSION

Cummings and Thompson (1971) showed that killer whale screams are effective in eliciting avoidance reponses in migrating grey whales, while comparable noise-bands and pure tones had little or no behavioral effect. The authors concluded that such whales apparently recognize the calls of the killer whale and flee from their source due to the potential danger of predation. Similar findings were obtained also by Fish and Vania (1971) when using the same sound in the presence of white whales. They noted avoidance, however, also during playback of a pulsed 2,500 Hz tone. Antipredatory behavior was also the conclusion reached by Frost et al. (1975) after noting rapid withdrawal behavior (sounding and porpoising in tight formation) by jackass penguins during playback of killer whale screams, as well as ". . . sweep frequency pulses . . ." of 600 to 2,500 Hz.

In the present study the subjects certainly withdrew from the killer whale scream; they withdrew also, however, from the other sounds as well. In fact, the sharks appeared clearly more responsive to the 500 to 4,000 Hz noise-band than the scream, both when the two signals were increased to response levels on separate days and when they were pitted against each other at one level on the same day. Although one cannot reject the possibility that the noise-band may be a super-optimal stimulus, it is reasonable to seek a more parsimonious justification for the results in a direction other than that of only a species-specific, predator-recognition process.

Fish and Vania (1971) did find pulsed pure tones effective at causing flight in white whales, and Frost et al. (1975) found pulsed sounds also effective in eliciting withdrawal in their subjects. Banner (1972) showed that withdrawal could be elicited by highly attractive sounds of prey and non-prey alike, and our results show that withdrawal can also be elicited by a variety of sounds. These findings, when viewed together, strongly suggest that some factor(s) other than recognizing a predator's phonation is mediating the process of withdrawal, a consequence of which results, nevertheless, in an anti-predator stratagem. One such factor is stimulus magnitude, another is the abruptness (i.e., rise time) in which a given magnitude of stimulation is achieved. These particular factors appear to have been critical for the withdrawal and "startle" by juveniles of the subject species in the field study conducted by Banner (1972); in fact, he reasoned that such sounds would resemble hydrodynamic sounds, generated by adult sharks, the major predators of juvenile sharks (Springer, 1963; 1967). It is perhaps not unreasonable that similar responses occur in other animals with predators in which a sudden, intense sound accompanies prey capture.

RATE AND MAGNITUDE OF SPL INCREASE

Rate of onset and/or magnitude of a stimulus has been found to elicit phonokinetic or phonotaxic responses (see Hinde, 1970, for definitions) in members of diverse groups of animals. To determine whether such factors are crucial to the withdrawal responsiveness of sharks, we conducted an additional experimental series.

METHODS AND MATERIALS

The 500 to 4,000 Hz noise-band was transmitted into the channel prior to testing at a level equal to that of broad-band ambient. The noise-band was then increased repeatedly with a rate of 96 dB/sec to successively higher levels, increasing in 3 dB steps. A minimal intensity at which the sharks would respond to the latter rate was chosen as that level at which three out of four possible withdrawals were obtained.

To determine if speed of change in the sound field influenced responsiveness, the noise-band was then increased during actual testing by that minimal magnitude, and the responsiveness was subsequently measured for three rates: 6, 24, and 96 dB/sec.

Unlike in the earlier phases of the study, the 500 to 4,000 Hz noise-band was produced by a random noise generator (H. H. Scott, Inc., 811B) in line with a band-pass filter (Krohn-Hite, 24 dB/oct. slope). This was done since the noise-band was transmitted into the channel prior to testing. Different rates of level gain were obtained using a gain-rate instrument (designed and constructed by Charles R. Gordon, electronics engineer of our school) at the output of a band-pass filter. A fixed-gain amplifier (Hewlett Packard, 466A) followed the gain-rate instrument to compensate for a 20 dB voltage drop at its output. The magnitude of the increase was controlled similarly by the gain-rate instrument (see Fig. 2 for diagram of instrumentation).

Sharks were invariably subjected to the peak intensity of a given signal at a distance 10 m from the speaker. This was accomplished by initiating transmission of the three different rates at three different distances from the criterion location. These were calculated from the: (1) increase in SPL, (2) rate of increase, and (3) patrolling speed of the approaching shark. Mean patrolling speeds were calculated from five measurements (time taked to swim 10 m, starting 5 m prior to the criterion distance and ending 5 m following it) for each shark used in these tests. As an example, for one subject, Icarus, swimming at a speed of 0.70 m/sec, the intensity increase of 18 dB was initiated when that shark reached 12.0 m from the loudspeaker (i.e., 2 m from the criterion distance) for the 6 dB/sec rate, 10.5 m for the 24 dB/sec rate, and 10.0 m for the 96 dB/sec rate. Determinations were aided by a grid of four lines, 1 m apart, stretching across the channel just above the water surface. Experiments were conducted from 2000 to 2300 h since all sharks were especially active at that time.

RESULTS

The minimal increase in intensity above ambient at which the lemon sharks responded to three of four playbacks of the 96 dB/sec rate was 18 dB. No withdrawal responses occurred during the four playbacks at 3, 6, and 9 dB. One response was elicited at 12 dB and two at 15 dB.

Seventeen increases were conducted for each of the three rates, and a similar number of no-increase controls were also carried out. No withdrawals were recorded during either the controls or when the rate of level gain was 24 dB/sec, and only three responses occurred at the 6 dB/sec rate of level gain. Ten withdrawals were recorded, however, at the 96 dB/sec rate, and this responsiveness was significantly greater than that to the slower rates (Fisher's Exact Probability Test, $P < 0.02$). Another criterion response recorded during testing was "veering." This particular motor pattern consisted of a shark swerving either to the left or right of the transducer at the moment of signal increase. When all withdrawals and "veerings" were totalled for the controls and tests, no responses were shown during the control periods and the 6 dB/sec rate, four were shown by increases possessing the 24 dB/sec rate, and two by increases possessing the 96 dB/sec rate.

The number of withdrawals shown to playbacks of the noise-band when its increase of 18 dB occurred at a rate of 96 dB/sec can be compared to those recorded during earlier playbacks of that same band using the same increase but without the signal being present before testing. In one such series, responses occurred in 18 out of 18 transmissions; in another, 16 out of 20 transmissions. This apparently reflects the shorter rise time and larger level gain that were used in the earlier tests.

The importance of signal-magnitude for evoking withdrawal was determined by keeping the rate of increase constant (96 dB/sec) and comparing responses for

increases of less than 18 dB (3 resps. out of 20 playbacks) with those of 18 dB (10 resps. out of 17 playbacks). A significant difference existed between these respective totals (Fisher's Exact Probability Test, $P < 0.02$).

Discussion

The significant findings obtained during this last phase of the study attest to the importance of at least two factors in bringing about rapid withdrawal in lemon sharks. It would appear in most instances that signal-magnitude and the abruptness by which that magnitude is achieved (i.e., rise time) act together in determining whether a shark will initiate approach, continue an approach, or suddenly withdraw (or veer) from a sound source.

These factors, as regards sounds, have been found to be crucial in eliciting various responses in numerous animals other than sharks (e.g., insects—Busnel, 1963; Minnich, 1925; bony fishes—Burner and Moore, 1953; Moore and Newman, 1956; birds—Shaw and Thiessen, 1954; and mammals—including man—Fleshler, 1965; Landis and Hunt, 1939; Strauss, 1929), and these factors are also known to be effective in other stimulus-classes (e.g., electrical—Hoffman et al. 1964; chemical—Smith and Bealer, 1975).

Schneiria (1939; 1959; 1965) was aware of such properties when he developed his approach-withdrawal theory to explain the ontogeny of behavior. The responses described in this report would be classed as W-responses, evoked by stimuli of high intensity, rapid onset, and irregular character. Since such responses may come to be evoked by other stimuli through appropriate conditioning, perhaps such modification may explain, in part, the responsiveness of the grey whales to the characteristic frequency and amplitude modulation of the killer whale scream (Cummings and Thompson, 1971).

Reasons for the equivocal findings mentioned in the introduction, relative to the usefulness of sounds in bringing about withdrawal in sharks, appear now more understandable. It is obvious that no sound can ever elicit withdrawal by any animal unless that animal can sense its occurrence. But once a sound has been detected and its direction is known, a shark has a number of options. If the sound has certain properties, the shark may approach; if the sound possesses other properties, the shark may withdraw. For a shout (or a similar sound) to be effective in warding off a shark, our findings suggest that it must be above a certain (unknown) magnitude. And since only certain test sounds elicited reasonably consistent withdrawals—and these were at differing magnitudes—the effective magnitude of a shout remains a moot question. In any case, the shout's relatively low SPL, coupled with transmission loss, strongly suggests that a shark would have to be very near such a source (within probably 2 or 3 m) before confronting an effective magnitude. The second factor, rise time, would be less of a problem in this case. Yet, if a sufficient rise time was not achieved, approach might well continue regardless of magnitude. Considering these variables, it is understandable why individuals have had different experiences in using sounds to ward off sharks. Undoubtedly, species differences probably also confound the problem. Our own experiences in such situations have been successful to date, but sounds have been used only when sharks (e.g., silkies, bulls) have approached us within a meter or two. Thus, some understanding of the withdrawal response by lemon (this report) and silky sharks (Myrberg et al., 1975; 1978) has been achieved; but we are still a long way from sufficiently understanding the phenomenon to allow reasonable certainty relative to its prediction and control.

ACKNOWLEDGEMENTS

LITERATURE CITED

Banner A. 1967. Evidence of sensitivity to acoustic displacements in the lemon shark, *Negaprion brevirostris* (Poey). Pages 265–273 *in* P. H. Cahn, ed. Lateral line detectors. Indiana University Press, Bloomington, 496 p.

———. 1971. Propagation of sound in a shallow bay. J. Acous. Soc. Am. 49: 373–376.

———. 1972. Use of sound predation by young lemon sharks, *Negaprion brevirostris* (Poey). Bull. Mar. Sci. 22: 251–283.

Brown, T. 1973. Sharks: the Search for a Repellent. Angus and Robertson, Sidney. 125 pp.

Burner, C. J., and H. L. Moore. 1953. Attempts to guide small fishes with underwater sound. Spec. Sci. Rep. U.S. Fish Wildl. Serv. 111: 1–38.

Busnel, R. G. 1963. On certain aspects of animal acoustic signals. Pages 69–111 *in* R. G. Busnel, ed. Acoustic behavior of animals. Elsevier Publishing Co., Amsterdam. 933 pp.

Cousteau, J. Y., and P. Cousteau. 1970. The shark: Splendid savage of the sea. Doubleday and Co., Garden City. 277 pp.

Cummings, W. G., and P. O. Thompson. 1971. Grey whales, *Eschrichtius robustus*, avoid the underwater sounds of killer whales, *Orcinus orca*. Fish. Bull. Fish Wildl. Serv. U.S. 69: 525–530.

———, J. M. Holzmann, and P. O. Thompson. 1975. Underwater sound pressure minima in bio-acoustic test tanks. Off. Nav. Res. Tech. Rep. TP 450. 40 pp.

Eibl-Eibesfeldt, I, and H. Hass. 1959. Erfahrungen mit Haien. Z. Tierpsychol. 16: 733–746.

Fish, J. F., and J. S. Vania. 1971. Killer whale, *Orcinus orca*, sounds repel white whales, *Delphinapterus leucas*. Fish. Bull. Fish Wildl. Serv. U.S. 69: 531–535.

Fleshler, M. 1965. Adequate acoustic stimulus for startle reaction in the rat. J. Comp. Physiol. Psychol. 60: 200–207.

Frost, P. G., P. D. Shaughnessy, A. Semmelink, M. Sketch, and W. R. Siegfried. 1975. The response of jackass penguins to killer whale vocalizations. S. Afr. J. Sci. 71: 157–158.

Hass, H. 1973. Men beneath the sea. St. Martin's Press, New York. 407 pp.

Hawkins, A. D. 1973. The sensitivity of fish to sounds. Pages 291–340 *in* H. Barnes, ed. Oceanography and marine biology, Vol. 11. George Allen and Unwin Ltd., London. 383 pp.

———, and D. N. MacLennan. 1976. An acoustic tank for hearing studies on fish. Pages 149–169 *in* A. Schuijf, and A. D. Hawkins, eds. Sound reception in fish. Elsevier Scientific Publishing Co., Amsterdam. 288 pp.

Hinde, R. A. 1970. Animal behaviour: a synthesis of ethology and comparative psychology. McGraw-Hill Book Co., New York. 876 pp.

Hobson, E. 1963. Feeding behavior in three species of inshore sharks. Pacif. Sci. 18: 171–194.

Hoffman, H. S., M. Fleshler, and P. L. Abplanalp. 1964. The startle reaction to electrical shock in the rat. J. Comp. Physiol. Psychol. 59: 53–58.

Kelly, J. C., and D. R. Nelson. 1975. Hearing thresholds of the horn shark, *Heterodontus francisi*. J. Acous. Soc. Am. 58: 905–909.

Kritzler, H., and L. Wood. 1961. Provisional audiogram for the shark, *Carcharhinus leucas*. Science, New York. 133: 1480–1482.

Landis, C., and W. A. Hunt. 1939. The startle pattern. Farrar and Rinehart, New York. 139 pp.

Martinez, D. R., and E. Klinghammer. 1970. The behavior of the whale *Orcinus orca*: a review of the literature. Z. Tierpsychol. 27: 828–839.

Minnich, E. D. 1925. The reactions of the larvae of *Vanissa antiopa* (Linn.) to sounds. J. Exp. Zool. 42: 443–467.

Moore, H. L., and H. W. Newman. 1956. Effects of sound waves on young salmon. Spec. Sci. Rep. U.S. Fish Wildl. Serv. 172: 1–19.

Myrberg, A. A., Jr., A. Banner, and J. D. Richard. 1969. Shark attraction using a video-acoustic system. Mar. Biol. 2: 264–276.

———, S. H. Ha, S. Walewski, and J. C. Banbury. 1972. Effectiveness of acoustic signals in attracting epipelagic sharks to an underwater sound source. Bull. Mar. Sci. 22: 926–949.

————, C. R. Gordon, and A. P. Klimley. 1975. Rapid withdrawal from a sound source by sharks under open-ocean and captive conditions. Off. Nav. Res. Tech. Rep. TR 75-5, 25 pp.

————. 1978. Rapid withdrawal from a sound source by open-ocean sharks. J. Acous. Soc. Am. 64: 1289–1297.

Nelson, D. R. 1967a. Hearing thresholds, frequency discrimination, and acoustic orientation in the lemon shark, *Negaprion brevirostris* (Poey). Bull. Mar. Sci. 17: 741–768.

————. 1967b. Cardiac responses to sounds in the lemon shark, *Negaprion brevirostris*. Pages 533–544 *in* P. W. Gilbert, R. F. Mathewson. and D. P. Rall, eds. Sharks, skates and rays. John Hopkins Press, Baltimore. 624 pp.

————. 1969. Meeting the shark underwater. Underwater Naturalist. 6: 13–26.

————, and S. H. Gruber. 1963. Sharks—attraction by low frequency sounds. Science, New York. 142: 975–977.

————, and R. H. Johnson. 1972. Acoustic attraction of Pacific reef sharks: effect of pulse intermittancy and variability. Comp. Biochem. Physiol. 42: 85–89.

————, R. H. Johnson, and L. Waldrop. 1969. Responses in Bahamian sharks and groupers to low frequency, pulsed sounds. Bull. So. Calif. Acad. Sci. 68: 131–137.

Olla, B. L. 1962. The perception of sound in small hammerhead sharks, *Sphyrna lewini*. M.S. thesis, University of Hawaii, 75 p.

Parvulescu, A. 1964. Problems of propagation and processing. Pages 87–100 *in* W. N. Tavolga, ed. Marine bioacoustics, Vol. 1. Pergamon Press, New York. 413 pp.

Schneiria, T. C. 1939. A theoretical consideration for approach-withdrawal adjustments in behavior. Psychol. Bull. 37: 501–502.

————. 1959. An evolutionary and developmental theory of biphasic processes underlying approach and withdrawal. Pages 1–43 *in* M. R. Jones, ed. Nebraska symposium on motivation, Vol. 7. University of Nebraska Press, Lincoln. 243 pp.

————. 1965. Aspects of stimulation and organization in approach-withdrawal processes underlying vertebrate behavioral development. Pages 1–74 *in* R. A. Hinde, D. Lehrman, and E. Shaw, eds. Advances in the study of behavior, Vol. 1. University of Nebraska Press, Lincoln. 320 pp.

Schevill, W. E., and W. A. Watkins. 1966. Sound structure and directionality in *Orcinus* (killer whale). Zoologica, N.Y. 51: 71–76.

Shaw, E. A., and G. J. Thiessen. 1954. High intensity sound as a repellent for mallard ducks and other water fowl. J. Acous. Soc. Am. 24: 141.

Smith, D. V., and S. L. Bealer. 1975. Sensitivity of the rat gustatory system to the rate of stimulus onset. Physiol. Behav. 15: 303–314.

Springer, S. 1963. Large sharks of the Florida-Carribean region. Pages 95–113 *in* P. W. Gilbert, ed. Sharks and survival. D. C. Heath and Co. Boston. 578 pp.

————. 1967. Social organization of shark populations. Pages 149–174 *in* P. W. Gilbert, R. F. Mathewson, and D. P. Rall, eds. Sharks, skates, and rays. John Hopkins Press, Baltimore. 624 pp.

Strauss, H. 1929. Das Zusammenshrecken. J. Psychol. Neurol. 84: 111–231.

Tavolga, W. N., and J. Wodinsky. 1963. Auditory capacities in fishes: pure tone thresholds in nine species of marine telosts. Bull. Am. Mus. Nat. His. 126: 177–240.

Wenz, G. M. 1962. Acoustic ambient noise in the ocean: spectra and sources. J. Acous. Soc. Am. 34: 1936–1956.

Rapid withdrawal from a sound source by open-ocean sharks

Arthur A. Myrberg, Jr., Charles R. Gordon, and A. Peter Klimley

Rosenstiel School of Marine and Atmospheric Science, University of Miami, Miami, Florida 33149
(Received 3 April 1978; revised 4 August 1978)

Studies undertaken in the Straits of Florida and the Tongue of the Ocean (TOTO), Bahamas, have established that silky sharks, *Carcharhinus falciformis*, while approaching a source of underwater sound, will withdraw rapidly from its vicinity if specified changes occur in the nature of the transmitted sound. These changes include: 1) an increase in level of the sound being transmitted (approximately 20 dB) and 2) an abruptness by which that level is achieved. Augmenting factors may include sudden changes in the spectral or temporal qualities of the transmitted sound. Although a biological sound (killer whale scream) could elicit clear withdrawal, it possessed no unique quality; rather, more simply constructed sounds, possessing only a restricted band of frequencies and lacking frequency-modulation, were equally effective. Habituation of the response was apparent during successive tests. All results closely followed those obtained on lemon sharks, *Negaprion brevirostris*, during a concurrent study (to be reported elsewhere). In the presence of added stimulants (chopped, fresh fish) withdrawal could be elicited in small silky sharks for only a short time. Limited testing of oceanic whitetip sharks, *Carcharhinus longimanus*, showed that extremely limited withdrawal could also be elicited in that species.

PACS numbers: 43.80.Lb, 43.80.Nd

INTRODUCTION

The aggressive behavior of sharks towards humans and their possessions has concerned scientists for many years. Within the last decade, efforts have been made to gain information on the biology of these animals so that their hazardous nature might be reduced in magnitude (Baldridge, 1973; Gilbert, 1970; Zahuranec, 1975). Despite this effort, our ignorance still centers on that aspect which relates most directly to that hazard—behavior. This is not surprising; observations on either the behavior *per se* of free-moving sharks or the effects of specific environmental factors upon that behavior often require lengthy and detailed monitoring. Yet, most species of sharks succumb rapidly in the laboratory and this constitutes a frustrating obstacle to further knowledge (Myrberg, 1976, Myrberg and Gruber, 1974). Field studies, however, provide an alternate approach, their data often providing valuable insight not only on behavioral and sensory capabilities but also on the ways that sharks use appropriate information in their natural environment.

During the last few years, various field studies have centered on the acoustical biology of selected species of both inshore and offshore sharks (Banner, 1968, 1972; Myrberg, 1972; Myrberg *et al.*, 1969, 1972, 1976; Nelson and Johnson, 1970, 1972; Nelson *et al.*, 1969) with emphasis directed at the rapid, oriented approach of such animals to an underwater sound source. Certain observations suggested, however, that under specific circumstances sharks may also withdraw from such a source as rapidly as they are attracted to it. To explore that point, a study was initiated which tested various biological and synthetic sounds at selected field locations, using as subjects epipelagic sharks of two species: the silky, *Carcharhinus falciformis* and the oceanic whitetip, *C. longimanus*. The basic idea underlying the study was that a successful predator, when approaching a source that is emulating properties of possible prey, may change its behavior when specific properties to which it is attending suddenly change. Since predatory actions, behavioral or otherwise, evidently require energy expenditure, an appropriate and highly effective mechanism would be one that could aid "decisions" relating to the conservation of such energy. This report deals with the results of the above-mentioned field study. Results from a closely allied study, involving an inshore species and conducted under a more controlled, but non-natural, setting, are discussed in part though reported in detail elsewhere (Klimley and Myrberg, 1978; Myrberg *et al.*, 1975).

I. MATERIALS AND METHODS

A. Initial phase

Four sounds were used during testing. The first was a recording of the scream of a killer whale (*Orcinus orca*) kindly provided by Dr. William C. Cummings (Fig. 1), which had previously elicited rapid avoidance
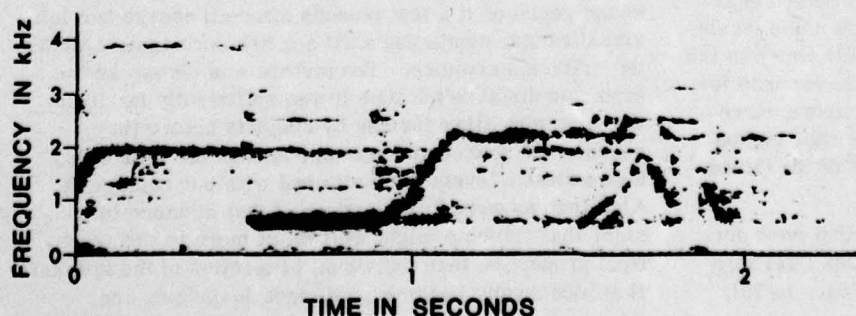

FIG. 1. The "scream" of the killer whale, *Orcinus orca*, used in tests of the initial phase (analyzing filter bandwidth—200 Hz.

in gray whales (Cummings and Thompson, 1971). Its structure was similar to that described and illustrated by Schevill and Watkins (1966). The scream was relatively rich in harmonics, containing energy between 500 and 4000 Hz (the included frequencies representing repetition rates and rapid changes thereof—see Schevill and Watkins, 1966). It consisted, mainly, of three glides, interrupted with sustained pitches of approximately 1900, 700, and 2200 Hz, respectively (the 700-Hz tone was approximately 3 dB louder than the other two). Two separate recordings were made; one with the sound (2.4 s in duration) in normal progression and repeating every 2.4 s, the other with the sound reversed in progression (to control for syntax) and also repeating every 2.4 s. Two synthetic sounds were also prepared, the first containing the frequency content (minus modulation) of the scream and the second being a pure tone of 800 Hz (near the peak amplitude of the scream). The duration of these sounds, as well as the interval between repetitions, was identical to those of the preceding sounds. Although sharks probably have an upper hearing limit not exceeding 1500 Hz (Banner, 1967, 1972; Kelly and Nelson, 1975; Kritzler and Wood, 1961; Myrberg et al., 1969; Olla, 1962; Nelson, 1967a, 1967b), frequencies above that point were not excluded since there is no evidence of such a limit for those species encountered during this study. The four recordings, placed on opposite tracks of two compact cassettes were produced so as to provide uniform, instant-peak levels on the playback recorder (used as a single-channel tape deck with signal output from the high end of the volume control). One uniform, instant-peak, pressure level provided the only reliable standard for playback, based on the differences that existed between the spectral energy levels of the respective sounds. This level, +58 dB/μbar re 1 m, was based on estimates of source levels for the killer whale scream, as well as the power capability of our experiment.

Although two inshore species, the lemon shark, Negaprion brevirostris, and the horn shark, Heterodontus francisci, have been shown to be sensitive to particle motion (Banner, 1967 and Kelly and Nelson, 1975, respectively), sound levels are given in terms of acoustical pressure. This was done for the following reasons: (1) Measurements of particle motion, using our accelerometers, demanded a stability of sea that was unattainable; (2) although measurement of pressure may not have provided a direct measure of sensitivity, it did allow repetitive testing at a consistent level of stimulation, with responses maintained at that level in the freefield situation; and, (3) the broadband nature of the test sounds precluded differentiating between near- and farfield effects. Inspection of ambient noise levels in both regions of testing and at comparable times of the year (see Myrberg et al., 1976) showed that source levels of all test sounds were at least 40 dB above corresponding spectrum levels of the noise in either region (Straits of Florida—initial phase; Tongue of the Ocean—second phase).

Instrumentation (Fig. 2) was basically that used during a previous bioacoustical study on sharks (Myrberg et al., 1976). An FM-direct recorder (Teac, R-70),

not shown in the figure, transmitted "attraction sounds" (rapid and irregularly pulsed signals in the 20–1000 Hz range) during the appropriate segments of each test period. It was coupled to the attenuator selector, as shown for the other recorders. A hand control allowing diver observers to change sound presentations at their location, was used only during the second phase (see below). During the initial phase that responsibility was undertaken by the instrument operator, onboard the accompanying vessel after appropriate notification by the observers.

All experiments included in this phase were carried out in the Florida Straits, approximately 15 kms east of Long and Triumph Reefs, Florida Keys, over depths of 300 m or more during January, June, and July. Only silky sharks, Carcharhinus falciformis, were encountered.

Upon reaching a selected location, vessel engines were stopped and two observers entered the water. They moved astern the vessel and then, while floating quietly, reported on the behavior of any sharks within visual range (approximately 25 m) via microphone. The initial "attraction sound" on any given day of testing was transmitted only if no sharks had been spotted for 15 min. Such transmission continued until an approaching shark reached the criterion distance of 10 m from the sound source (positioned at a depth of 10 m). That sound then ceased and one of the four test sounds began 3 or 4 s later from the same source. If, during the brief interim, the subject had moved beyond the criterion distance, e.g., when approaching at or near tangent, the test was discontinued. Also, if no subject reached that distance within 3 min of entering visual range, testing was again discontinued. A new sequence, involving the attraction sound followed by one of the test sounds, began again only if sharks were not seen for 5 min. Although the paradigm resulted in instances where data were not obtained despite sharks being in visual range, it did provide a reasonable level of standardization among all tests and controls. When a test sound did commence, the subject usually had reached a distance of approximately 8 m from the source. Its behavior was closely monitored until it left visual range; where possible, reports included the activities of other nearby sharks. Comments by the instrument operator, a time-reference signal, and sounds from a monitoring hydrophone were also recorded simultaneously for later analysis. A test sound was usually repeated only four times during a given test and was never repeated more than six times. Once a test sound had been transmitted, the attraction sound replaced it a few seconds after all sharks had left visual range, continuing until a shark once again reached the criterion distance. Ten meters was chosen as the criterion distance because it was sufficiently far from the source to allow turning by subjects before they reached the source and yet near enough for reasonably high acoustic levels to be attained with our equipment. Also images were small enough at that distance to consider that subjects might well react more to the acoustical properties than the visual properties of the speaker. Both observers became proficient in judging the
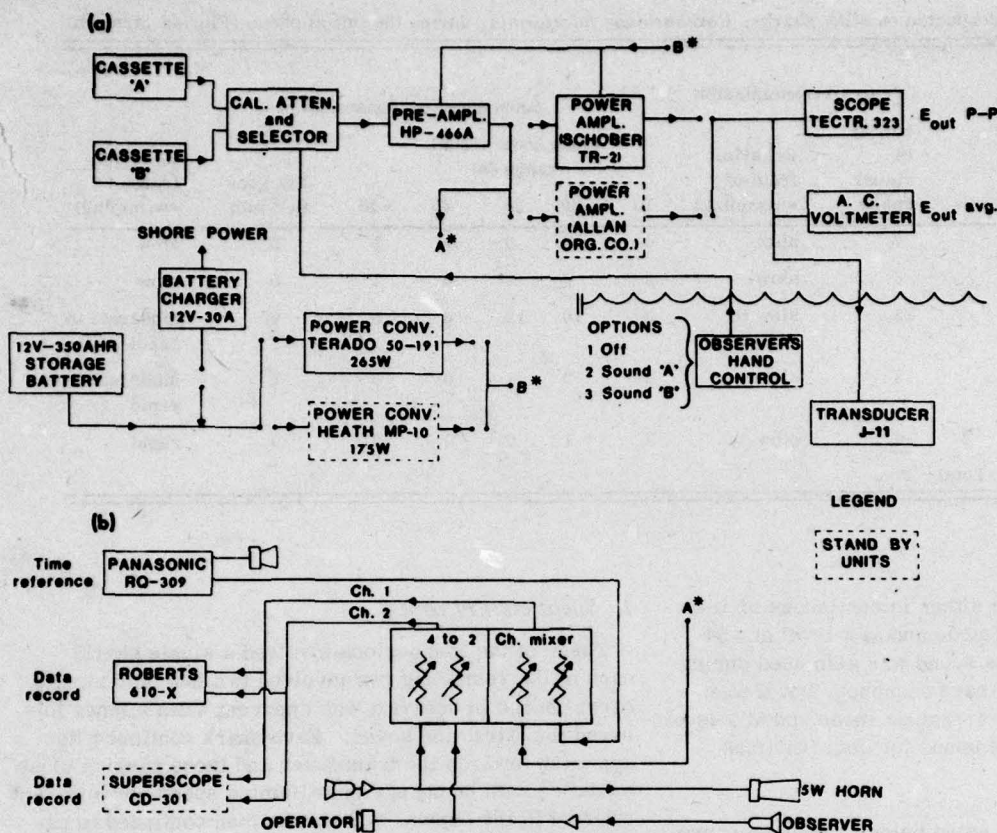
(a)

(b)

FIG. 2. Block diagram of instrumentation used during testing. (a) Sound transmission and control; (b) communication and data recording.

criterion distance, as well as shorter distance prior to actual testing.

The most reasonable measure of responsiveness was the time between onset of a test sound and when sharks left visual range (the individual reaching the criterion distance left visual range within a few seconds of any nearby sharks). That measure allowed effectiveness among the various sounds tested to be compared.

Testing emphasized the killer whale scream since this appeared initially to be "biologically" interesting to approaching sharks. This did not preclude gaining information on the remaining sounds, however. To insure that point, of the eight experimental series constituting this phase (a series being all test sequences run on a given day), each test sound held either the initial, second, or last test position within, at least, three different series, each series being separated from another by at least 10 days. Additionally, five silent-control periods were also interspersed among the respective tests. These periods involved witholding transmission of any sound once a shark reached the criterion distance, silence being maintained until all sharks had moved out of visual range. This provided a comparison of the levels of responsiveness during periods of transmission and periods of silence.

Occasionally only two test sounds were transmitted during a half-day period. This was due either to sharks

not reappearing for an hour or more after cessation of a test sound or to "breaks" interspersed between sequences so that effects of prior testing would be minimal (Klimley and Myrberg, 1978; Myrberg et al., 1969; Nelson, 1965).

B. Second phase

Ten series (119 tests) were conducted in the Tongue of the Ocean (TOTO), Bahamas (24° 30'N, 77° 20'W) during November. Eight (104 tests), involving silky sharks, were either near a large buoy (MONAB) moored over a depth of approximately 2000 m, 14 km east of the AUTEC Base, Fresh Creek, Andros or offshore of Green Cay, an uninhabited island, located approximately 80 nautical miles southeast of the MONAB. Two series (15 tests) conducted also at the MONAB, involved oceanic whitetip sharks.

The only test sound used during this phase was synthetic (150–600 Hz band). This change in test sound was based on data from the initial phase and those from another study (Klimley and Myrberg, 1978) which strongly suggested that the killer whale scream, though effective in bringing about withdrawal, was not unique, and that a simpler sound, possessing a narrowband of frequencies, could also be effective. Thus, we chose a sound that was easily synthesized and transmitted via the direct recorders used during the initial phase. During actual

TABLE I. Summary of tests conducted on silky sharks, *Carcharhinus falciformis*, during the initial phase (Florida Straits).

| Test-sound (control) | No. of repetitions | Sharks in visual range | Behavior (rate of swimming) | Gone from visual range (s) | | | | | Not gone in 3 min | Behavior (rate of swimming) |
| | | Prior to transmission | | Subsequent to transmission | | | | | | |
				10	20	30	40	>40		
(Silent control)	5	7	slow	0	0	0	1	1	5	slow
Pure tone	5	6	slow	0	0	0	0	1	5	slow
Killer whale scream	14	25	slow to moderate	3	10	12	0	0	0	moderate to rapid
Killer whale scream played backwards	3	5	slow	3	0	1	0	0	1	moderate to rapid
Noiseband	3	4	slow	3	1	0	0	0	0	rapid
	Total: 47									

testing, the sound was used either in continuous or ir-regular (as in morse code) mode and at a level of +54 dB/μbar *re* 1 m. The same sound was also used during the "attraction" segment of each sequence, but it was then transmitted only in the irregular mode and at a level of +34 dB/μbar. Using one sound for both functions simplified all operations.

Except for the variations noted below, the general pro-cedures for, and restrictions to, testing followed those used during the initial phase. Sounds were turned on and off by the control box, held by one diver observer (Fig. 2). This allowed sounds to be changed more rapidly than during the initial phase. Also, the test sound was trans-mitted usually for only 10 s. This period was sufficient to allow most sharks to reach the limit of visibility and yet brief enough to prolong the time before probable habituation to the signal.

Subsequent to all regular testing, procedures were changed during two series, both involving silky sharks. In one, small amounts of chopped, fresh fish were added to the water during all transmissions. This was done to determine if withdrawal could be effected even in the presence of such an added stimulant. In the second se-ries, not only was chum added to the water but a small, freshly killed fish was also tied by a 1-m length of line to the transducer. During this series, signal onset often occurred even though a given shark was well within the 10-m criterion distance. This was due to (1) highly in-creased swimming speeds and, (2) often erratic and un-predictable movements by individuals within 10 m of the source.

II. RESULTS

A. Initial phase

Behavioral differences were clearly evident among the subjects, depending on the situation confronting them once the attraction sound ceased during a given sequence (Table I).

1. Silent control period

Three of the five periods involved a single shark; each of the remaining two involved two individuals. No overt change in behavior was apparent when silence fol-lowed the attraction sound. Each shark continued its approach towards the transducer and those passing close by did so with no change in swimming speed nor apparent interest in the object. All sharks then continued to pa-trol slowly, either moving toward the observers and then away or moving in a rather wide arc in a nonpredictable direction. Of the seven sharks encountered, five were still patrolling within visual range 3 min after the attrac-tion sound had ceased; one left visual range shortly after 2 min and one left within 40 s of the onset of the period. The high speed and directed movement suddenly shown by the latter individual, indicated that something beyond visual range had taken its interest.

2. Pure tone

Four of the five periods involved a single shark; one involved two sharks. The pure tone was ineffective in changing the behavior of any individual. During trans-mission, all sharks continued their approach to the source with no change in swimming speed and each passed close by the source with no apparent interest. All subjects were visible throughout the period of trans-mission, and all but one remained in sight 3 min after onset of the test sound. The exceptional shark moved slowly out of visual range approximately 90 s after onset of the test sound, its behavior revealing no apparent causal relationship with the sound.

3. Three remaining sounds (Killer whale scream, scream played backwards, and the noiseband)

The behavior of sharks following the onset of trans-mission of the remaining sounds, was far different from that just summarized. At the moment when one of these sounds began, a few sharks turned within 1 or 2 s in a narrow arc away from the transducer; others, heading directly at the source, veered sharply. Still others, ap-

TABLE II. Summary of tests conducted on silky sharks, *Carcharhinus falciformis*, during the second phase (Tongue of the Ocean, Bahamas).

Total series completed	8
Total tests conducted	104
Number of series, using test-sounds without added stimulants	6
Number of tests conducted	51
Number of sharks within 8–10 m of sound source	63
Distribution of responses (provided below)	
Number of silent-control periods	18
Number of sharks within 8–10 m of sound source	23
Number of sharks showing rapid withdrawal	0
Number of series, using test sounds in the presence of added stimulants	2
Number of tests conducted with sharks within 3–10 m of sound source	53
Distribution of responses (provided in Fig. 4)	

Distribution of withdrawal responses throughout successive tests in series using test-sounds only.

Successive tests w/in series	No. of series involved	No. of sharks w/in 8–10 m of sound source	No. of sharks showing rapid withdrawal	% of sharks showing rapid withdrawal
1–3	6	20	17	88
4–6	4	16	10	62
7–9	4	12	7	58
10–12	2	4	1	25
13–15	1	6	1	16
16–18	1	5	0	0
		Total 63		

proaching the source tangentially, also turned away, but in a wider arc than that noted in the previous cases. None showed dramatic responses or rapid, disoriented behavior. All did show two features in common, however; each increased its speed and moved on a straight-line course out of visual range such that all but one had disappeared from view within 30 s of the sound onset. The direction of withdrawal signified that all animals were aware of the direction to the sound source. These activities differed greatly from those noted when sharks were within visual range, and events held little or no interest for them. They then patrolled slowly and, though occasionally approaching objects, usually moved in ever-widening circles until they were lost from view. The time it took to attract the animals back to the vicinity of the source after appropriate test and control periods also differed. As was often seen during previous studies on attraction, sharks approached an active sound source almost invariably within seconds or a few minutes, following a brief, quiet period. Similar time periods occurred also following either transmission of the pure tone or the silent control periods. In contrast, sharks usually did not appear in visual range sooner than 20 min after any of the three effective sounds was transmitted, even though the attraction sound began shortly thereafter. Oftentimes, they did not reappear at the site for an hour or more. Considering drift by the vessel, those individuals which finally did appear after such a lengthy in-

terval may well have been sharks other than those involved in the previous test.

a. Killer whale scream. Eight of the 14 periods involved a single shark; two involved two sharks, three involved three sharks and one involved four sharks. All 25 animals encountered during these tests left visual range within 30 s of test onset; 13 were gone within 20 s.

b. Killer whale scream, played backwards (control for syntax). Two periods involved a single shark and one involved three. In the last case, all had left visual range within 10 s and, in one of the other periods, the subject disappeared within 30 s. The single exception to a shark reacting in the normal manner to the effective sounds occurred during playback of this sound. This lone individual, remaining in visual range for 3 min, 35 s after sound onset, was the largest shark (over 3 m in length) attracted during this phase. Reasons for this exception are unknown; but a relationship appeared to exist between the size of a shark and its speed of withdrawal. It is possible that this exception reflected that relationship.

c. Noiseband (500–4000 Hz). Three sharks encountered during tests of this sound left visual range within 10 s of sound onset; one left within 20 s (two tests involved one shark each and one test involved two sharks). The rapid responses occurred regardless of the position held by the test sound in its respective series. In fact, only one series involved test sounds being used in five successive sequences and, in that particular case, the last sound transmitted was the noiseband.

4. Summary

No essential difference was found among the three effective sounds eliciting withdrawal. Similarity of response to these quite different sounds strongly suggested that certain acoustical features could probably be dismissed as playing a major role in eliciting the withdrawal response. First, the temporal order of acoustical events, as noted in the natural scream, had no apparent value since that order was reversed in the "backward scream" and nonexistent in the noiseband. Second, the specific frequency modulation of the scream probably played no essential role, based on the responses shown to the noiseband which had no such modulation. Specific amplitude modulations could also be dismissed as probable factors, based on the same reasoning. Finally, the specific time envelope of the effective sounds probably was unimportant since the pure tone possessed that same envelope. The pure tone appeared as ineffective in eliciting withdrawal as it was in eliciting attraction (Myrberg *et al.*, 1969; Richard, 1968).

B. Second phase

1. Silky sharks

The results obtained on silky sharks at the MONAB and at Green Cay were pooled because of their similarity (Table II). Twenty-three sharks were encountered during 18 silent controls; no shark withdrew rapidly from the transducer during such periods. Fifty-one tests were
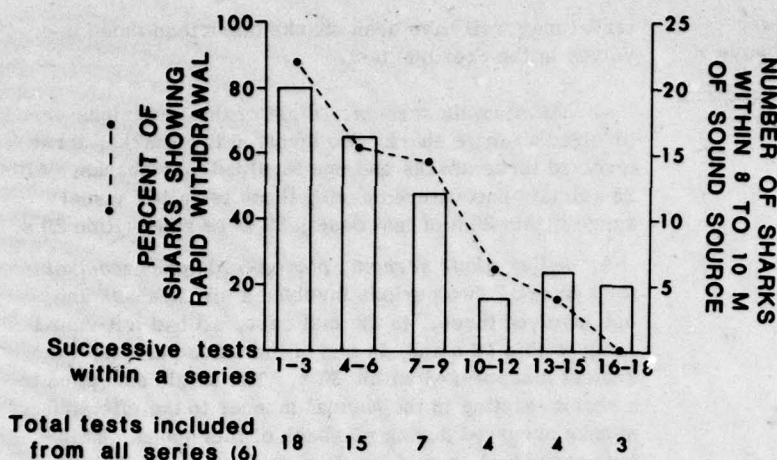
FIG. 3. Distribution of withdrawal responses by silky sharks, *Carcharhinus falciformis*, throughout successive tests of the second phase. Eliciting stimulus was a noiseband, 150–600 Hz, with sudden onset and a sound pressure level of + 54 dB/ubar *re* 1 m.

distributed among six series (5–18 per series). In those cases where rapid withdrawal was elicited by a test sound, animals often reappeared at the test site 10–30 min after cessation of that sound. Although this interval was shorter than that usually noted for those members of the species encountered in the Florida Straits, it was much longer than the minute or so it took for such animals to reappear after a silent control period. The number of tests per series during this phase allowed us to examine the loss in effectiveness of the test sound over successive periods among members of the same population of sharks. Evidence for this came from repeated encounters with individuals having distinctive scars and fin irregularities. Results (Table II and Fig. 3), suggested that habituation was indeed affecting responsiveness in the manner noted during acoustic attraction (see Myrberg *et al.*, 1972, 1976). Despite this downward cline over successive sequences, it is noteworthy that a reasonably high percentage of withdrawal was recorded during early tests even though the attraction sound and

the test sound differed in only one important variable—sound level, i.e., the test sound was 20 dB louder. It should be mentioned that the test sounds were invariably louder than attraction sounds since a preliminary study had shown that reducing the level of a test sound by 20 dB subsequent to cessation of an attraction sound did not affect behavior. Although test sounds were transmitted in one of two modes, continuous or irregular, neither appeared any more nor any less effective in eliciting withdrawal. Yet, since all series did not deal symmetrically with them, final judgment as to the relative effectiveness of each must be withheld.

Results from the final two series (7 and 8) involved test sounds transmitted in the presence of added stimulants (Fig. 4). Nine successive withdrawals involving a single individual (approximately 1.5 m long), were elicited during series 7 before the sound failed to elicit such a response. Shortly thereafter, repeated transmission failed to elicit any withdrawal. In series 8, the pres-

(a)

CRITERION DISTANCE FOR STIMULUS CHANGE ~10 M

TIME SINCE BEGINNING OF TEST SERIES (MIN)

(b)

CRITERION DISTANCE FOR STIMULUS CHANGE VARIABLE

TIME SINCE BEGINNING OF TEST SERIES (MIN)

● = Onset of attraction sound
(150–600Hz) (+34 dB/μb)

+ = Rapid turning away from transducer

− = No change in approach response

| = Continuous sound (150–600Hz) for 4 to 10 s;
20dB (+54dB/μb) above attraction sound

⁞ = Rapid, irregularly pulsed sound (150–600Hz) for 4 to 10 s; 20dB (+54dB/μb) above attraction sound
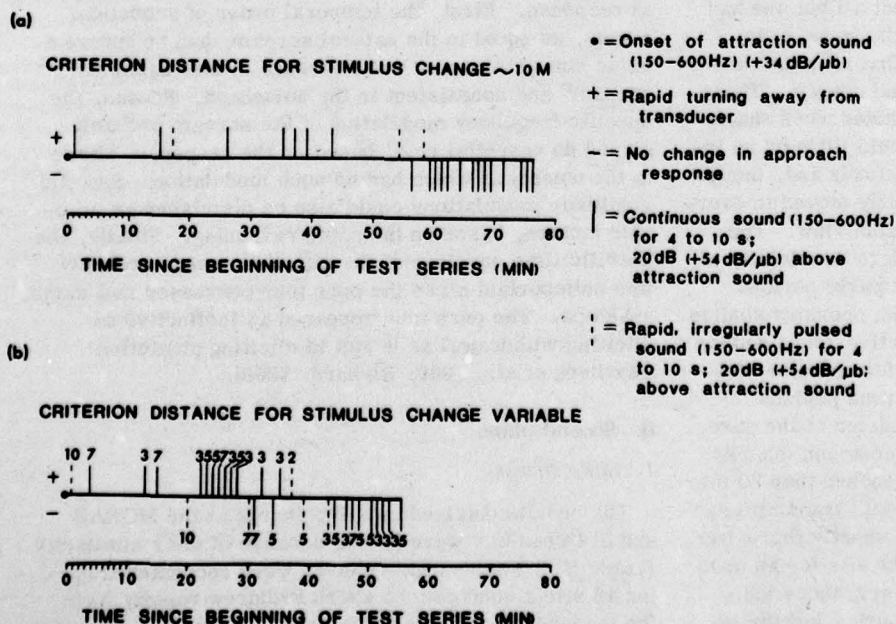
FIG. 4. Behavior of silky sharks, *C. falciformis*, during the two series in which added stimulants were present (second phase). The sudden onset of the test sound represented a 20–dB increase in the sound field; (a) series 7 involved a single shark, chopped bait used; (b) series 8 involved two sharks—distances and responses shown apply only to that individual closest to the source. Chopped bait was used, fish were tied to transducer. Numbers indicate distance (m) of shark from source when stimulus was changed.

TABLE III. Summary of the tests conducted on oceanic white-tip sharks, *Carcharhinus longimanus*, during the second phase (Tongue of the Ocean, Bahamas).

Total series completed	2
Total tests conducted	15
Number of sharks within 3–10 m of sound source	15
Distribution of responses (provided below)	
Number of silent-control periods	3
Number of sharks within 10 m of sound source	5
Number of sharks showing rapid withdrawal	0

Distribution of withdrawal responses throughout successive tests

Successive test sequences	Criterion distance (in m)	No. of series involved	No. of sharks, w/in 3–10 m of sound source	No. of sharks showing rapid withdrawal	% of sharks showing rapid withdrawal
1–2	10	2	4	3	75
3–4	5–7	2	4	1	25
5–6	3–7	2	4	0	0
7–8	3–7	2	3	0	0
			Total 15		

ence of chum and the freshly killed fish both resulted in faster and more erratic movements of the two sharks (each being approximately 1.5 m long). Such movements, as well as their reluctance to withdraw beyond 10 m approximately 20 min into the series often resulted in the test sound being turned on when the nearest shark was only 3–5 m from the source. Although the test sound was reasonably effective in protecting the fish at short range during the first 28 min of the series (11 turns in 12 approaches), its effectiveness rapidly declined thereafter. By 39 min into the series, withdrawal was no longer elicited despite 11 presentations of the test sound. During that period, the fish was often attacked. These two series, though incomparable with one another, did show that withdrawal can be elicited acoustically from relatively small, silky sharks for a short time, even in the presence of certain stimulants. Such responses do wane, however, after varying periods of time, apparently dependent on the nature of the added stimulant.

2. Oceanic whitetip sharks

Two whitetip sharks (each approximately 2 m long) appeared together during the initial tests of two series. The attraction sound had been on in each case for approximately 2 min, and though two silky sharks appeared briefly about the same time in one case, no others appeared at any time during either series. In each series, only one whitetip approached the criterion distance prior to a given test, invariably the same individual. The other individual moved slowly about at varying distances (15–20 m) from the source during the initial sequences of each series, moving out of visual range around the midpoint of each series. Thereafter, it reappeared erratically during the remaining attraction sequences but did not approach the transducer. The only times that the straggler approached the transducer were during the two silent-control periods that followed the second and fourth transmission of the attraction sound during one

series. In these cases, the straggler followed the other shark close by the transducer, neither shark showing any apparent interest in the object. The results therefore largely reflect the responses of only one member of each pair (Table III). Withdrawals were elicited only during the initial sequences of both series, i.e., during the first of seven tests in one series, lasting 18 min and during the first three of eight tests in the other series, lasting 15 min. Thus, attempts were made to elicit response at distances closer than 10 m from the transducer after the second test of each series, i.e., exposing the animal to higher sound levels. With one exception, the third test of one series at 7 m, such attempts failed. Previous encounters with members of the species showed them to be extremely dangerous; therefore, safety precautions precluded adding any stimulants during testing.

Oceanic whitetip sharks were rarely encountered by us under conditions that allowed any type of testing. Because its usual habitat is far from any land mass, the species has only recently been found to be readily attracted to a variety of underwater sounds (Myrberg *et al.*, 1976). Although results pointed out that under specific conditions, at least some members of the species will withdraw from a sound source, their withdrawal response differed markedly from that seen in silky sharks. Initial withdrawal involved a veering of the body away from the transducer at the onset of the test sound. In one case, the sound was in continuous mode but, in the other, irregular. Individuals veered about 90° from their former course and headed to the limit of visibility. At that moment, the attraction sound began and each shark returned to the criterion distance (10 m) within 3 min, which was much earlier than that experienced with silky sharks. The second and third recorded withdrawals in one series again involved turning away from the transducer as the test sound began. However, the angle of veer was less than 90° and the shark did not withdraw as rapidly as noted during the initial withdrawal. There was no appreciable increase in speed as it moved away from the source. After 4 min of one series and 6 min of the other, the test sound elicited no further withdrawals during 11 tests. Each shark continued its head-on course toward the transducer and turned only slightly from that course when within approximately 2 m of it, passing it by within 1 m. Testing ceased after five such approaches in about 10 min during one series and six approaches in 12 min during the other.

III. DISCUSSION

The combined results from both phases have established that under specified conditions, shark withdrawal can be effected by various sounds. These signals need not possess qualities unique to any biological sound. The close temporal association between the abrupt onset of an effective sound and withdrawal suggests that a sudden and sufficient change in acoustical events at that moment are critical to elicit the response. That change was effective in only one direction, however. A sudden reduction in sound level subsequent to attraction had no apparent behavioral effect. Effective sounds were different temporally and spectrally from the attraction

sound during the initial phase, but not during the second phase. Differences were present, however, in the sound levels (20 dB) of those signals used during the second phase and, though the peak levels were the same among the sounds of the initial phase, differences in loudness were assuredly present, based on differences in their spectral energy levels. Thus, our tests could not ascertain whether changes in temporal or spectral qualities of a sound are alone sufficient to elicit withdrawal. But it is not unreasonable to consider such changes as augmenting those which appear to be direct causal factors. These are (1) increased loudness (level) of an effective sound over that of the immediately preceding attraction sound and, (2) the abruptness of that increase. During the "attraction" segments of this study, rapidly approaching sharks moving at speeds of 1–3 m/s were probably experiencing an increase in sound level approaching 1 dB/m (assuming spherical spreading) just prior to reaching the 10-m criterion distance. The sudden onset of a test sound at that distance during the second phase of this study, therefore, resulted in at least a tenfold jump in the level that normally would have been experienced during approach.

It is noteworthy that a concurrent study of adult lemon sharks, has shown these same two factors were also critical for elicitng withdrawal in the members of that species (Klimley and Myrberg, 1978). Although the abruptness by which a signal attains a given level was not varied systematically during the present study, it was duly considered in the concurrent study. The time taken to reach an effective level was correlated with the effectiveness of a given test sound with peak responsiveness being seen when the onset was essentially instantaneous.

The ineffectiveness of pure tones in eliciting withdrawal in both studies (500- and 800-Hz tones were used) remains enigmatic. Although laboratory evidence from a variety of species within the family, *Carcharhinidae*, strongly suggests that such tones were heard at the distances indicated, perhaps reduced hearing ability in that range resulted in the level being insufficient to effect withdrawal.

Rapid withdrawal by sharks from sound sources has not gone unnoticed by others. Eibl-Eibesfeldt and Hass (1959), as well as Nelson (1969) noted that reef sharks could be repelled by loud yelling. Hobson (1963) and Hass (1973) in contrast, found that ineffective while Brown (1973) also mentioned withdrawal from the sources of various sounds. Banner (1972) likewise reported that juvenile lemon sharks fled at the onset of certain sounds. He hypothesized that short-interval sounds provided a smooth increase of their signal levels as a shark approached. Thus, attraction continued even right up to the source. But sounds of an impulsive nature (i. e., a single pulse) or those possessing long intervals (e. g., in seconds) would result in sudden jumps in level to be perceived and, when that level exceeded some point, startle and flight would occur. Banner's data appeared to bear out the idea.

The point at which approach changed to rapid withdrawal was experimentally determined in adult lemon sharks

to be 21–24 dB above broadband ambient for a rapidly pulsed, broadband sound (Klimley and Myrberg, 1978). A similar point, 20 dB, arbitrarily chosen for the second phase of the present study, was also effective with silky sharks. Considering the variables involved, it is understandable that a sound, such as an underwater shout, would be ineffective in repelling an approaching shark in most instances. Not only may response be dependent on a factor such as the size of the animal concerned but the level of an underwater shout, coupled with transmission loss, most probably requires that an approaching shark be very near before an effective level would be attained. We have used such a sound successfully on silky and bull sharks, but only after such animals approached to within 1–3 m.

The two factors that appear important in bringing about withdrawal in sharks through acoustical means—the sound level and the abruptness whereby that level is achieved—are also responsible for eliciting startle or withdrawal among animals from widely diverse groups. For relevant discussions, see Busnel (1963), Minnich (1925)—insects; Burner and Moore (1953), Chapman (1976), Moore and Newman (1956)—bony fishes; Shaw and Thiessen (1954)—birds; and Fleshler (1965), Landis and Hunt (1939), Strauss (1929)—mammals, including man. Yet, differences are found between and within species ranging from the intensity of response to the stability of response over successive trials. Such differences were also apparent between members of the two species confronted during the present study. For example, withdrawal was far more limited in oceanic whitetip sharks than in silky sharks. Accordingly, similar variation among individuals and among species must be expected in future experiments.

ACKNOWLEDGMENTS

Baldridge, H. D. (1973). "Shark attack against man," Tech. Rep., Office of Nav. Res., Contract N00014-73-C-0252, Mote Marine Laboratory, Sarasota (unpublished).

Banner, A. (1967). "Evidence of sensitivity to acoustic displacements in the lemon shark, *Negaprion brevirostris* (Poey)," in *Lateral Line Detectors*, edited by P. H. Cahn (Indiana University, Bloomington), pp. 265–273.

Banner, A. (1968). "Attraction of young lemon sharks, *Negaprion brevirostris*, by sound," Copeia 4, 871–872.

Banner, A. (1972). "Use of sound in predation by young lemon sharks, *Negaprion brevirostris* (Poey)," Bull. Mar. Sci. 22, 251–283.

Brown, T. (1973). *Sharks—The Search for a Repellent* (Angus and Robertson, Sidney).

Burner, C. J., and Moore, H. L. (1953). "Attempts to guide small fishes with underwater sound," Spec. Sci. Rep., U. S. Fish. Wildl. Serv. 111, 1–38.

Busnel R. G. (1963). "On certain aspects of animal acoustic signals," in *Acoustic Behavior of Animals*, edited by R. G. Busnel (Elsevier, Amsterdam), pp. 66–111.

Chapman, C. J. (1976). "Some observations on the reactions of fish to sound," in *Sound Reception in Fish*, edited by A. Schuijf and A. D. Hawkins (Elsevier, Amsterdam), pp. 241–253.

Cummings, W. C., and Thompson, P. O. (1971). "Gray Whales, *Eschrichtius robustus*, avoid the underwater sounds of killer whales, *Orcinus orca*," Fishery Bull., U. S. Fish. Wildl. Serv. 59, 525–530.

Eibl-Eibesfeldt, I., and Hass, H. (1959). "Erfahrungen mit Haien," Z. Tierpsychol. 16, 733–746.

Fleshler, M. (1965). "Adequate acoustic stimulus for startle reaction in the rat," J. Comp. Physiol. Psychol. 60, 200–207.

Gilbert, P. (1976). "An evaluation of some chemical, biological, and physical agents tested for their effectiveness as shark deterrents," in *Sharks and Man: A Perspective*, edited by W. Seaman, Jr. (Fla. Sea Grant Program, Rep. 10), pp. 19–20.

Hass, H. (1973). *Men Beneath the Sea* (St. Martin's, New York).

Hobson, E. (1963). "Feeding behavior in three species of inshore sharks," Pac. Sci. 18, 171–194.

Kelly, J. C., and Nelson, D. R. (1975). "Hearing thresholds of the horn shark, *Heterodontus francisci*," J. Acoust. Soc. Am. 58, 905–909.

Klimley, A. P., and Myrberg, A. A., Jr. (1978). "Acoustic stimuli underlying withdrawal from a sound source by adult lemon sharks, *Negaprion brevirostris* (Poey)," Bull. Mar. Sci. (in press).

Kritzler, H., and Wood, L. (1961). "Provisional audiograms for the shark, *Carcharhinus leucas*," Science 133, 1480–1482.

Landis, C., and Hunt, W. A. (1939). *The Startle Pattern* (Farrar and Rinehart, New York).

Minnich, E. D. (1925). "The reactions of the larvae of *Vanissa antiopa* (Linn.) to sounds," J. Exp. Zool. 42, 443–467.

Moore, H. L., and Newman, H. W. (1956). "Effects of sound waves on young salmon," Spec. Sci. Rep., U. S. Fish Wildl. Serv. 172, 1–19.

Myrberg, A. A., Jr. (1972). "Using sound to influence the behavior of free-ranging marine animals," in *Behavior of Marine Animals—Current Perspectives in Research*, edited by H. E. Winn and B. L. Olla, (Plenum, New York), Vol. 2, pp. 435–468.

Myrberg, A. A., Jr. (1976). "Behavior of sharks—a continuing engima," Nav. Res. Rev. 29, 1–11.

Myrberg, A. A., Jr., and Gruber, S. H. (1974). "The behavior of the bonnethead shark, *Sphyrna tiburo*," Copeia 2, 358–374.

Myrberg, A. A., Jr., Banner, A., and Richard, J. D. (1969). "Shark attraction using a video-acoustic system," Mar. Biol. 2, 264–276.

Myrberg, A. A., Jr., Gordon, C. R., and Klimley, A. P. (1975). "Rapid withdrawal from a sound source by sharks under open-ocean and captive conditions," Tech. Rep., Office of Nav. Res., Contract N00014-67-A-0201, Rosenstiel School of Marine and Atmospheric Science, TR75-5, Univ. of Miami, Miami, Florida (unpublished).

Myrberg, A. A., Jr., Gordon, C. R., and Klimley, A. P. (1976). "Attraction of free-ranging sharks to low frequency sound, with comments on its biological significance," in *Sound Reception in Fish*, edited by A. Schuijf and A. D. Hawkins (Elsevier, Amsterdam), pp. 205–228.

Myrberg, A. A., Jr., Ha, S. J., Walewski, S., and Banbury, J. C. (1972). "Effectiveness of acoustic signals in attracting epipelagic sharks to an underwater sound source," Bull. Mar. Sci. 22, 926–949.

Nelson, D. R. (1965). "Hearing and Acoustic Orientation in the Lemon Shark, *Negaprion brevirostris* (Poey) and Other Large Sharks," Ph. D. dissertation (University of Miami, Coral Gables, Florida).

Nelson, D. R. (1967a). "Hearing thresholds, frequency discrimination, and acoustic orientation in the lemon shark, *Negaprion brevirostris* (Poey)," Bull. Mar. Sci. 17, 741–768.

Nelson, D. R. (1967b). "Cardiac responses to sounds in the lemon shark, *Negaprion brevirostris*," in *Sharks, Skates and Rays*, edited by P. W. Gilbert, R. F. Mathewson, and D. P. Rall (Johns Hopkins, Baltimore), pp. 533–544.

Nelson, D. R. (1969). "Meeting the shark underwater," Underwater Nat. 6, 13–26.

Nelson, D. R., and Johnson, R. H. (1970). "Acoustic studies on sharks, Rangiroa Atoll, July 1969," Tech. Rept., Office of Nav. Res., Contract N00014-68-C-0318, Long Beach, Calif. State College, Found. Rep. No. 2 (unpublished).

Nelson, D. R., and Johnson, R. H. (1972). "Acoustic attraction by Pacific reef sharks: Effects of pulse intermittency and variability," J. Comp. Biochem. Physiol. 42A, 85–95.

Nelson, D. R., Johnson, R. H., and Waldrop, L. G. (1969). "Responses in Bahamian sharks and groupers to low frequency, pulsed sounds," Bull. South Calif. Acad. Sci. 68, 131–137.

Olla, B. (1962). "The Perception of Sound in Small Hammerhead Sharks, *Sphyrna lewini*," Master's thesis (University of Hawaii, Honolulu, Hawaii).

Richard, J. D. (1968). "Fish attracted with pulsed, low-frequency sound," J. Fish. Res. Board Can. 25, 1441–1452.

Schevill, W. E., and Watkins, W. A. (1966). "Sound structure and directionality in *Orcinus* (killer whale)," Zoologica 51, 71–76.

Shaw, E. A., and Thiessen, G. J. (1954). "High intensity sound as a repellent for mallard ducks and other waterfowl," J. Acoust. Soc. Am. 24, 141.

Strauss, H. (1929). "Das Zusammenschrecken," J. Psychol. Neurol. 84, 111–231.

Zahuranec, B., Editor. (1975). *Shark Research, Present Status and Future Direction*. ONR Rep. ACR-208, Dept. of Navy, Arlington, 51 pp.

MANDATORY DISTRIBUTION LIST

FOR UNCLASSIFIED TECHNICAL REPORTS, REPRINTS, & FINAL REPORTS
PUBLISHED BY OCEANOGRAPHIC CONTRACTORS
OF THE OCEAN SCIENCE AND TECHNOLOGY DIVISION
OF THE OFFICE OF NAVAL RESEARCH
(REVISED NOV 1978)

Office of Undersecretary of Defense
1   Research & Engineering (ELS)
ATTN: Col. Joe Friday
Room 3D129
Pentagon
Washington, D.C. 20301

Office of Naval Research
800 North Quincy Street
Arlington, VA 22217
3   ATTN: Code 483*
1   ATTN: Code 460
2   ATTN: 102B

1   Res Rep (if any)

Commanding Officer
Naval Research Laboratory
Washington, D.C. 20375
6   ATTN: Library, Code 2627

12**   Defense Documentation Center
Cameron Station
Alexandria, VA 22314
ATTN: DCA

Commander
Naval Oceanographic Office
NSTL Station
Bay St. Louis, MS 39522
1   ATTN: Code 8100
1   ATTN: Code 6000
1   ATTN: Code 3300

1   NODC/NOAA
Dode D781
Wisconsin Avenue, N.W.
Washington, D.C. 20235

*   Add one separate copy of
Form DD-1473

**   Send with these 12 copies two completed froms DDC-50,
one self addressed back to the contractor, then the other
addressed to ONR, code 480.

REPORT DOCUMENTATION PAGE		READ INSTRUCTIONS BEFORE COMPLETING FORM
1. REPORT NUMBER	2. GOVT ACCESSION NO.	3. RECIPIENT'S CATALOG NUMBER
4. TITLE (and Subtitle) Underwater sound: a review of its effects on sharks.		5. TYPE OF REPORT & PERIOD COVERED Technical April 1978 - Dec. 1979
		6. PERFORMING ORG. REPORT NUMBER
7. AUTHOR(s) Arthur A. Myrberg		8. CONTRACT OR GRANT NUMBER(s) N00014-76-C-0142
9. PERFORMING ORGANIZATION NAME AND ADDRESS Rosenstiel School of Marine & Atmospheric Science, University of Miami, 4600 Rickenbacker Cswy., Miami, Florida 33149		10. PROGRAM ELEMENT, PROJECT, TASK AREA & WORK UNIT NUMBERS NR104-587
11. CONTROLLING OFFICE NAME AND ADDRESS Office of Naval Research, Code 480 Department of the Navy NSTL Station, Mississippi 39529		12. REPORT DATE December 1979
		13. NUMBER OF PAGES 51 pages
14. MONITORING AGENCY NAME & ADDRESS(If different from Controlling Office)		15. SECURITY CLASS. (of this report) Unclassified
		15a. DECLASSIFICATION/DOWNGRADING SCHEDULE

16. DISTRIBUTION STATEMENT (of this Report)

Approved for public release, distribution unlimited

17. DISTRIBUTION STATEMENT (of the abstract entered in Block 20, if different from Report)

Approved for public release, distribution, unlimited.

18. SUPPLEMENTARY NOTES

19. KEY WORDS (Continue on reverse side if necessary and identify by block number)

acoustics - <u>Carcharhinus</u> - shark behavior
animal behavior- Marine Biology-shark biology
attraction by sound - sensory biology - withdrawal from sound

20. ABSTRACT (Continue on reverse side if necessary and identify by block number)

Reprints are provided of three published studies on underwater sound and its effects on the behavior of sharks. Subjects include those species of sharks which have been attracted to sound sources, the physical factors which appear to be important or unimportant for an acoustical attractant, and the behavior of sharks in the vicinity of a sound source. Emphasis is directed also at those qualities of sound that promote withdrawal from a sound source by three species of sharks, <u>Carcharhinus</u> <u>falciformis</u>, <u>C</u>. <u>longimanus</u> and

20. _Negaprion brevirostris._